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Variation in Clutch and Litter Size in New World Reptiles

By

Henry S. Fitch

UNIVERSITY OF KANSAS
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24 May 1985

Variation in Clutch and Litter Size in New World Reptiles

BY

HENRY S. FITCH

Museum of Natural History
and
Department of Systematics and Ecology
The University of Kansas
Lawrence, Kansas 66045 USA

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INTRODUCTION

During the past two decades, much interest in the subject of reptilian reproduction has developed, and detailed studies of many species have been carried out. As a result of these studies, it has been well established that reproductive parameters such as clutch or litter size, number of broods per season, and time required for development from natality to sexual maturity all vary intraspecifically and are subject to geographic variation.

Geographic variation in number of eggs per clutch or young per litter has been alleged by Klauber (1956) in *Crotalus viridis* and other rattlesnakes, by McCoy and Hoddenbach (1966), Pianka (1970) and others in *Cnemidophorus tigris,* by Fitch (1970, 1980) in *Diadophis punctatus* and other species, by Goldberg (1971) in *Sceloporus jarrovi,* by Tinkle and Ballinger (1972) and Vinegar (1975) in *Sceloporus undulatus,* by Moll (1973) in *Chrysemys picta,* by Goldberg (1974) and Jameson and Allison (1976) in *Sceloporus occidentalis,* by Montevecchi and Burger (1975) in *Malaclemys terrapin,* by Petokas and Alexander (1980) in *Chelydra serpentina* and by Howard (1974) in *Phrynosoma cornutum.* However, no general summary of such geographic variation has been published. The purpose of the present report is to summarize available data concerning clutch and litter size in American reptiles, to compare trends in turtles, lizards and snakes, and to attempt to identify environmental factors which control such variation. Especially, search is made for trends of latitudinal change and their climatic bases; and comparisons of latitudinal and altitudinal trends are made.

It is recognized that clutch and litter size is subject to individual variation, that older females produce larger broods than younger females, and that larger females produce more young than those that are smaller; that year-to-year fluctuations in weather and other environmental factors can cause annual changes in the average clutch of a local population, and that local environmental factors can have such important effects that neighboring populations sometimes differ markedly in their clutch sizes. All those are confounding factors that might obscure or overshadow geographic variation if it existed. Therefore, the study of geographic variation in clutch and litter size has turned out to be far more difficult than it seemed at the outset. The present study addresses the following specific questions: 1. Can evidence of geographic variation in clutch and litter size be discerned? 2. Are there broad trends with groups of species varying geographically in somewhat parallel fashion? 3. Is geographic variation in clutch or litter usually clinal? 4. Is length of growing season, by controlling number of clutches, instrumental in determining size of clutch, and is this reflected in altitudinal and latitudinal trends, or trends from relatively aseasonal to seasonal climates (e.g., those with dry seasons)? 5. Are populations on continental islands different in clutch and litter size from mainland relatives? 6. In the kinds of variation mentioned above, are the main groups of reptiles, such as turtles, lizards, snakes and crocodilians, detectably different from each other in their responses?

METHODS AND MATERIALS

Data are here assembled concerning clutch or litter size and its geographic variation in 137 of the common and widely distributed species of New World reptiles, and an additional 28 satellite species that are their geographic representatives. Some 33,600 clutches and litters are represented; about 94% of these are extracted from publications of other authors, while 2000 clutch records of 44 species are based upon my own first-hand observations. The latter group include my field records from the University of Kansas Natural History Reservation (1948–1982), the San Joaquin Experimental Range (1938–1947) and elsewhere, and also include records of museum speci-

mens in the University of California Museum of Vertebrate Zoology (MVZ), the American Museum of Natural History (AMNH) and the natural history museums of the University of Colorado (CU), the University of Kansas (KU) and the University of Texas (TU). Examinations of museum specimens were made mainly in the early 1960s, during the course of my study of reproductive cycles in snakes and lizards (Fitch, 1970).

Data are organized and presented in a series of species-accounts under RESULTS. Also, the sources of all records used are shown in Appendices I and II. The former includes records of clutches or litters that I personally gathered both from the field and from museum specimens. Appendix II documents all records from published papers (including my own) in abbreviated form with authors' initials, year of publication, and separate counts of clutches (or their means, if large series were involved). Geographic origin of the specimens is shown only in Appendix I since this information can be extracted for the records in Appendix II by referring back to the original publications.

In each species account available records are allocated in two or more groups in order to show geographic differences such as island versus mainland, northern versus southern, or eastern versus western. For each sample the mean, range, and standard error are shown, if all are available. Some of the species accounts included are based on such source material as abstracts of the papers presented at national meetings and provide little or no specific data. For *Thamnophis marcianus,* for instance, only Karge's (1982) statement of general trends is available, and in a dozen other cases sample size was not indicated although samples apparently were substantial. Question marks are here used where sample size is not known.

Some commonly used methods of determining clutch or litter size are: counts of eggs found in natural nests; counts of eggs laid or young born by females held in confinement; and, from dissections, counts of oviducal eggs or embryos, counts of yolked ovarian follicles, and counts of corpora lutea. However, there are potential sources of error in each of these approaches. The female may deposit only part of her complement in a nest; or two or more females may leave their eggs together in a communal nest, and a nest found with eggs may have lost some of the original complement to predators. Various investigators have found that, within a species, ripe follicles average somewhat more numerous than oviducal eggs or embryos, and these in turn are somewhat more numerous than eggs laid or young born, because there is some mortality at each stage of development. Each type of record was included in the present compilation, and admittedly some error was introduced by this heterogeneity. The reductions from follicles to oviducal eggs to neonates or eggs laid, however, are considered to be relatively minor sources of error, usually only a few per cent, and much less than differences that might be caused by different average sizes of females in compared samples, or differences caused by time of collection (i.e. early season vs late season, or "good" year vs "bad" year). Where such non-geographic factors are believed to have influenced the differences between geographic samples, this possibility is mentioned in the discussion.

The many authors whose works are cited as sources of information about clutch or litter size represent a wide diversity of research interests. Some of the best local series of records come from the work of investigators (Cieslak, 1945; Fox, 1948; Bauman and Metter, 1977; Osgood, 1978; Yntema, 1979; Arnold, 1981) who were concerned with the physiological or genetic aspects of reproduction, and mentioned litter size casually, perhaps neglecting to report infertile eggs or atretic follicles which have significance in the present context. For some of the more prolific species, authors have published notes from time to time extolling the efforts of individual females that produced record clutches or litters. Such maximum figures could distort geographic means and therefore have been intentionally excluded in my comparisons.

In the following brief species accounts I have attempted to show the evidence for or against geographic variation in clutch or

litter size in some 137 species of common turtles, lizards, snakes and crocodilians. For most of the species here included, figures are available from medium-size or large local series from at least one part of the range. Where such adequately large series are available for comparison, I have generally excluded and disregarded isolated records of individuals. In other instances samples consist of composites of records well scattered in time and space. Small local series have, wherever possible, been combined with other records to increase sample size. Statistics for the separate samples such as standard error of the mean, provided by the original author, are retained in the listings of Appendix II.

For snakes, much of the older literature concerning clutch and litter size, especially for the northeastern United States, was summarized by Wright and Wright (1957) and for the sake of brevity, I have cited these authors rather than including the numerous old and sometimes obscure publications in the literature cited. Many such records from Wright and Wright, cited in my paper (Fitch, 1970) on reproductive cycles in lizards and snakes, could not be used in the present context because no geographic area was designated.

From the trend of the records, I suspect that in general every geographic population differs from others in mean clutch or litter size, with effects of many genetic and environmental factors inextricably blended. In some instances relatively small samples are here cited, although these cannot in themselves justify positive conclusions, in the belief that they will eventually have usefulness, in combination with other data, for analyzing trends. In local series variance is usually high because of greater productivity in larger females than in smaller ones, greater productivity early in the season than later, and change from year to year. This high degree of variance renders it difficult to demonstrate geographic differences at, say, the 95% level of significance.

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RESULTS

Accounts of species

TURTLES

The reproductive strategies of turtles are influenced by the facts that the rigid, armor-encased body has little capacity for expansion to accommodate a large clutch mass, that aquatic or semi-aquatic habits in most render them weightless in a water medium and allow carrying of the developing eggs with minimum handicap, that greater tolerance for low temperature than possessed by most other reptiles permits penetration into north temperate regions where growing seasons are short, and that sexual dimorphism is usually pronounced. All are oviparous. As a general rule the female is larger than the male, and in some species she may average as much as 15 times the male's bulk. The relatively large size of the female may be an adaptation to increase her egg capacity. However, in sea turtles, which are the most prolific of all reptiles, females are only slightly larger than males. In North American freshwater turtles there are parallel geographic trends in various species, involving change from south to north in: 1) delayed maturity; 2) increased body size; 3) reduction in number of clutches to only one or two; 4) increase in size of egg; 5) increase in number of eggs per clutch. The more southern populations of the species showing these trends usually produce several clutches per season.

Caretta caretta. The nesting of this almost cosmopolitan sea turtle has been studied in various parts of the world. Samples of clutch sizes from the western hemisphere suggest a latitudinal trend.

Temperate (North Carolina, Smith Island, 33° 50′N) $\bar{x} = 120$ in ?
Temperate (South Carolina, Cape Romain, 33°07′N) $\bar{x} = 117 \pm 0.2$ in 393
Temperate (Georgia, Little Cumberland Island, 30°52′N) $\bar{x} = 120$ in 1897
Subtropical (Florida, Sanibel and Captiva islands, 26°30′N) $\bar{x} = 110$ (44-172) in 46
Tropical (South America, Colombia, Buritaca Beach, 11°15′N) $\bar{x} = 107$ (58-163) in 185

At Little Cumberland Island individual females were found to nest as many as six times per season. At Buritaca Beach, Colombia, Kaufmann (1975) found a two-year nesting cycle in individual females, whereas in more northern populations a three-year cycle may prevail. At Buritaca nesting began in late April, peaked in June, and continued into August, with up to four successive nestings observed for the same female. There seemed to be a trend toward increasing clutch size with successive renestings.

Chelonia mydas. Although the green turtle is cosmpolitan in tropical and warm temperate seas, its nesting beaches are well isolated and there is probably little interbreeding between populations. Important differences between populations in adult body size, clutch size, reproductive cycle and renesting interval have been discovered (Hirth, 1971). Four samples are available from the Western Hemisphere.

Subtropical, Florida, 26°N $\bar{x} = 129.6$ (91-158) in 27
Tropical, Costa Rica, Tortuguero, 10°30′N $\bar{x} = 112.3$ (18-193) in 2040
Tropical, Pacific Costa Rica, Playa Naranjo, 11°N $\bar{x} = 87$ (67-107) in 10
Tropical South America, Surinam, 6°N $\bar{x} = 142$ (87-226)

At Tortuguero almost 84% of the breeding females are "recruits" in their first season of reproduction (Bjorndal, 1980). These recruits produce an average of 2.7 clutches with 111.4 eggs per clutch, whereas older remigrant females average 116.8 eggs and 3.4 clutches. Total egg production per reproductive season averages 301 in recruits vs 397 in remigrants. Most typically, females return to the nesting beaches after a three-year interval, but sometimes two or four years elapse.

Since the tropical populations produce both larger and smaller clutches than those of the more seasonal climate of subtropical Florida, the effect of climate is not evident.

The large average clutch in the Surinam turtles is correlated with large body size, as these are among the biggest green turtles in the world, according to Hirth (op. cit.). They average approximately 112.5 cm in

carapace length (N = 60), vs 100 for Tortuguero (N = 200), 107 for Ascension Island (N = 200), 97.5 for Sarawak (N = 200), and 95.5 for southern Yemen (N = 225). Mean clutch size has been calculated as 115.5 for Ascension Island, 110 for Australia, and 104.7 for Sarawak, Borneo. Playa Naranjo females averaged much smaller, 82.9 cm in 73. Relatively small female size and small clutch at Playa Naranja supports the supposition that the Pacific green turtle is a distinct species, *Chelonia agassizi*.

Chelydra serpentina. Several medium to large samples are available to show clutch size in this large chelydrid.

Northwestern (South Dakota)
$\bar{x} = 49.0$ (31-87) in 102
North-central (Wisconsin, Dodge County)
$\bar{x} = 44.0$ (?-85) in 70
Northeastern (New York, Ontario)
$\bar{x} = 39.1$ (16-66) in 115
Central (Tennessee) $\bar{x} = 19.9$ (12-42) in 20
Southeastern (northern Florida)
$\bar{x} = 16.6$ (14-20) in 8

A marked increase from south to north is suggested, with possibly some increase also from east to west. The three sizable series here combined for the northeastern sample varied markedly, as follows: Jefferson County, New York $\bar{x} = 30.9 \pm 2.8$ (16-59) in 16; Onondaga County, New York, 46.0 in 53; Algonquin Park, Ontario, 33.9 ± 10.0 (18-66) in 46. The wide variation in these means is surprising, and needs to be clarified with further sampling.

Chrysemys picta. Many samples are available to show clutch size in this common and widely distributed emydid. However, most are from the eastern parts of the range. Unfortunately, some of the samples are small and may obscure trends (Fig. 1). The highest figures are from the most northern area, Saskatchewan. Mean clutch size is notably higher in the northern half of the range than in the southern half, from which samples are few and small. Also, there is a possible trend of increase from east to west, so that clutches from New Mexico average more than twice as many eggs as those from the southeastern United States, but the relatively high altitudes of localities in New Mexico perhaps render them climatically comparable to more northern latitudes, at least in length of growing seasons.

In the southern part of the range, Louisiana and Arkansas, sexual maturity is attained by males at an age of 2 or 3 years, and by females at 4 years, at carapace lengths of 60-65 mm, and 100 mm, respectively (Moll, 1973). In contrast, in the northern part of the range, in Wisconsin, male maturity is attained in 4 or 5 years at lengths of 95-100 mm, and female maturity at 7 or 8 years and 135-140 mm. Population dynamics, hence, change markedly over the range, with reproductive potential greatly increased southward, but the relatively large northern turtles produce more eggs per clutch.

A part of the Illinois sample was reported upon by Tucker (1978) who studied the turtles at Lake Sara, a small body of water in east-central Illinois. Tucker found that clutch size varied from 5.9 to 9.9 eggs in four different samples (N = 5, 5, 9, and 14) from different parts of the lake, and he concluded that different environmental conditions, even within such a small area, could affect clutch size in different samples.

Dermochelys coriacea. This giant sea turtle is one of the most prolific reptiles. However, in almost every clutch many eggs are infertile and yolkless. In 27 clutches from French Guiana, Fretey (1980) found 25% of the eggs to be infertile. In Malaya, Hendrickson (1962) found 11 of 95 clutches to be entirely infertile, and from the remaining 84 clutches with a total of 7,490 eggs, only 3,699 hatchlings emerged. A combination of infertile eggs, embryonic mortality, and failure of some hatchlings to escape from the nest accounted for their 51% loss between laying and emergence. Data gathered from several populations in different parts of the world seem to show that there are important differences in adult size and in clutch size, but more samples are needed to clarify trends. Because of the meagerness of samples from the Americas, two Old World samples are here included with them.

South temperate, South Africa, Natal
$\bar{x} = 136$ (30 abnormal) in ?
Tropical, 11°30′N, Pacific Nicaragua
$\bar{x} = 111$ (17-179 with 48 abnormal) in 27
Tropical, 10°N, Costa Rica, Tortuguero
$\bar{x} = 97$ (73-145, 31.5 abnormal) in 6

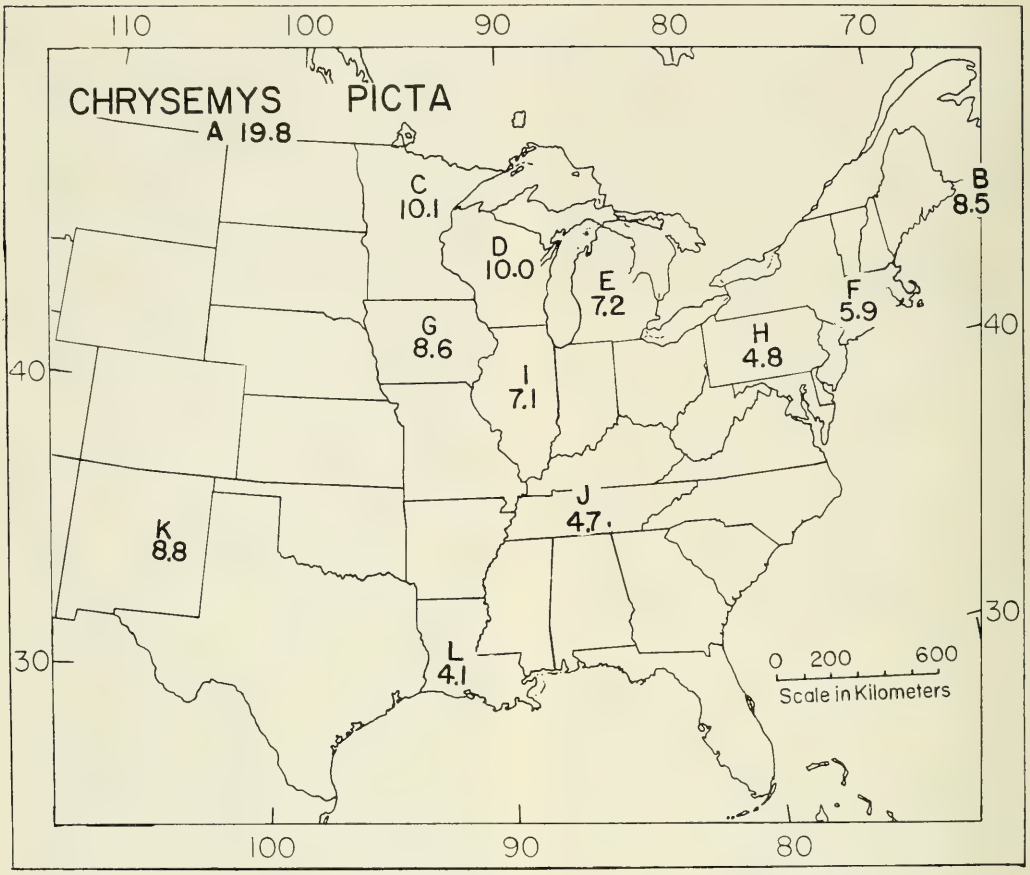

FIG. 1.—Map showing geographic variation in clutch in *Chrysemys picta*. A. Sasketchewan **19.8** (17-23) number unknown; B. Nova Scotia **8.5** (5-11) in 26; C. northern Minnesota **10.1** (5-19) in 23; D. Wisconsin **10.0** (3-16) in 151; E. Michigan **7.2** (2-11) in 182; F. Connecticut **5.9** (5-7) in 7; G. Iowa **8.6** in 59; H. Pennsylvania **4.8** (3-6) in 15; I. Illinois **7.1** in 81; J. Tennessee **4.7** (2-19) in 42; K. New Mexico **8.8** (2-15) in 46; L. Louisiana **4.1** (1-6) in 41.

Equatorial, Asia, Malaya, Trengganu
$\bar{x} = 88$ (many abnormal) in 95
Equatorial, South America, French Guiana
$\bar{x} = 114.5$ (30.2 abnormal) in 27

Seemingly clutch size tends to be higher in regions removed from the equator where climates are more seasonal.

Emydoidea blandingii. This large, secretive emydid is northern in distribution. Its habits and ecology have been made much better known through recent studies in Ontario and Michigan.

Ontario, St. Lawrence River, Thousand Islands, 43°N $\bar{x} = 12.2$ (8-18) in 50
Southeastern Michigan, George Reserve, 42°N $\bar{x} = 10.0$ (3-15) in 90
Illinois, 40°N 6 to 10 eggs (Cahn, 1937)

These records suggest a northward increase in clutch, but the latitudinal distance involved is not great. In Ontario, Petokas (1984) found that clutch size is strongly correlated with female body size (but not with age), and in individual females clutch size tends to increase slowly throughout life.

Eretmochelys imbricata. One large clutch sample and one small sample are available for the hawksbill turtle, with but little evidence of geographic change.

Costa Rica, Tortuguero, 10°30′N
$\bar{x} = 161.1$ (53-206) in 57
Guiana, 6°N $\bar{x} = 158.1 \pm 4.7$ (139-176) in 7

Gopherus polyphemus. The available data indicate no latitudinal change in clutch size, and the geographic range is not extensive.

Southwestern Georgia
$\bar{x} = 7.0 \pm 1.7$ (4-12) in 47
Florida $\bar{x} = 5.2$ (1-9) in 41

Graptemys ouachitensis. Along the Mississippi River in western Wisconsin, Vogt (1980) found an average clutch of 10.5 (N = 65), but Webb (1962) found a much lower mean of 5.84 in a small sample (N = 6) from Lake Texoma, far to the south. Collins (1982) recorded Kansas clutches of 5 and 12 and if these are included in the southern sample, its average is 6.5.

Kinosternon bauri. Two samples of clutches are available for this small mud turtle.

Northern (northern Florida)
$\bar{x} = 2.7 \pm 0.9$ (1-5) in 48
Southern (central Florida)
$\bar{x} = 2.3 \pm 0.2$ (1-3) in 12

Northward increase in clutch size is possible but unlikely. Geographic variation would be on a minor scale, as the range is limited to peninsular Florida and adjacent southern Georgia.

Kinosternon flavescens. The four samples available to show clutch size in this small kinosternid seem to show well defined geographic variation.

Northern (Nebraska) $\bar{x} = 5.7$ (4-7) in 13
Central (N Texas, central Oklahoma)
$\bar{x} = 5.0$ (4-5) in 21
Southern (New Mexico) $\bar{x} = 3.6$ (1-6) in 29
Southwestern (Sonora) $\bar{x} = 4.5$ in 80

In Great Plains populations body size is markedly smaller than it is in those from Sonora. The Great Plains turtles produce only one clutch annually whereas those in Sonora produce two clutches and have larger eggs.

Kinosternon hirtipes. This small mud turtle is found in the United States only in the Big Bend region of western Texas. Its populations occur chiefly on the Pacific slope and interior basins of western Mexico, often in disjunct ranges. The following figures are all derived from Iverson's (1981) study.

Northern (Rio Santa Maria, Chihuahua)
$\bar{x} = 2.9$ (2-5) in 30
Central (Rios Carmen, Conchos, Papigochic, Nazas, Aguanaval in Chihuahua, Coahuila, Durango, Zacatecas)
$\bar{x} = 4.4 \pm 0.2$ (1-6) in 19
Southern (Durango, San Luis Potosi, Jalisco, Michoacan, Guanajuato)
$\bar{x} = 4.1 \pm 0.4$ (1-9) in 17

The number of annual clutches were estimated at 3 or 4 for the northernmost localities and only 2 for the southernmost. Possibly there is northward decrease in clutch size.

Kinosternon subrubrum. The scattered records of clutches of this small kinosternid provide some evidence of geographic variation. No series is available from the northern part of the range, but two early records by Nichols (1947) of clutches with 4 and 7 eggs on Long Island suggest clutches there may average larger than in the southern part of the range, where clutches of 1, 2 or 3 eggs are common.

Western (Arkansas, Oklahoma)
$\bar{x} = 4.0$ (1-6) in 49
Eastern (Savannah River, South Carolina; Georgia, Alabama)
$\bar{x} = 3.1$ (2-4) in 197
Southwestern (Louisiana)
$\bar{x} = 2.1$ (1-3) in 12
Southeastern (northern Florida)
$\bar{x} = 3.5$ (2-5) in 13

If there are geographic trends, they are not made clear by these figures.

Malaclemys terrapin. Three samples of clutch size for this coastal emydid show a well defined trend.

Northern (New Jersey)
$\bar{x} = 10.3 \pm 1.2$ (4-18) in 49
Southern (Louisiana)
$\bar{x} = 8.5 \pm 0.6$ (5-12) in 11
Southernmost (Florida)
$\bar{x} = 6.7 \pm 0.4$ (5-10) in 14

Increased clutch size northward is indicated.

Podocnemis expansa. This giant pleurodiran river turtle of tropical South America has an extensive geographic range, and its seasonal schedule is known to vary geographically. In the Orinoco region egg-laying, occurring mainly on islands in the river, is timed to the lowest water level, usually in February (Roze, 1964). In the Rio Trombetas of Para, Brazil, just south of the equator, egg-laying, likewise timed to the lowest water level, peaks nearly four months earlier, in October, and clutch size is somewhat larger.

Orinoco, 8°N
$\bar{x} = 84.9$ (sample size not recorded)
Trombetas, 0°20′S $\bar{x} = 93.1$ in 5582

In the Trombetas region Alho and Padua (1982), working with enormous samples, found clutches to average somewhat smaller

(76-91) in the initial (first to ninth) and terminal (21st to 24th) days of the laying season than in the middle part (tenth to 20th days) when clutches averaged 96 to 98. Clutch size is correlated with female size both within and between populations. Orinoco females were found to have mean carapace length of about 60 cm, vs 66 cm in Trombetas females.

Pseudemys scripta. Several substantial samples of clutches for this abundant emydid are available, clearly demonstrating geographic variation.

Northern (southern Illinois) $\bar{x} = 9.5$ (4-18) in 217
Northern (Tennessee, Reelfoot Lake) $\bar{x} = 10.5$ (5-22) in 47
East-central (South Carolina, Savannah River) $\bar{x} = 7.7$ (2-17) in 121
Southeastern (northern Florida) $\bar{x} = 7.5 \pm 0.7$ (4-9) in 8
West-central (Oklahoma, Lake Texoma) $\bar{x} = 8.8$ (1-12) in 6
Southwestern (southern Louisiana) $\bar{x} = 7.2$ (4-11) in 188

Reduction of clutch from north to south may occur. The South Carolina sample is from Gibbons (1982) who found that clutches averaged markedly larger, 10.2 ± 0.4 (6-17) $N = 48$, in Parr Pond, artificially heated by effluvients from an atomic reactor, than in Ellerton Bay, 6.1 ± 0.2 (2-15) $N = 73$, in a more natural situation. The Parr Pond females grew more rapidly, and to much larger size and clutch size was found to be positively correlated with size of female. Likewise, in southern Illinois, Thornhill (1982) found larger body size, earlier maturity and larger clutch (12.5 ± 0.4) in the artificially heated waters of Lake Baldwin than in more natural situations nearby (11.09 ± 0.4).

Tropical representatives of the group, formerly considered conspecific but now placed in different species, grow to much larger size, produce larger clutches, and have more clutches per season (Moll and Legler, 1971).

Sternotherus minor and **S. depressus.** Tinkle (1958) in his revision of the group gave a figure for average clutch size in *S. m. peltifer* and for *S. depressus,* but indicated sample size only in *S. m. minor.* Presumably all his samples were small. The only adequate samples are those of *minor* from Florida reported by Cox and Marion (1978) and Iverson (1978).

Northern (Virginia to Mississippi, sbsp. *peltifer*) $\bar{x} = 7.0$
Western (northern Alabama, sp. *depressus*) $\bar{x} = 5.5$
Southeastern (Florida, sbsp. *minor*) $\bar{x} = 2.7$ in 6
Southeastern (northern Florida, sbsp. *minor*) $\bar{x} = 2.4 \pm 0.09$ (1-4) in 107
Southeastern (Florida, sbsp. *minor*) $\bar{x} = 2.4$ in 131

Sternotherus odoratus. Tinkle (1961) in an early study showed that clutch size increases from south to north in this small kinosternid. The following figures correlating clutch size with isotherm zone are from his report.

Isotherm zone 45-50	$\bar{x} = 5.5$ in 10
Isotherm zone 50-55	$\bar{x} = 3.5$ in 2
Isotherm zone 55-60	$\bar{x} = 3.0$ in 2
Isotherm zone 60-65	$\bar{x} = 2.8$ in 4
Isotherm zone 65-70	$\bar{x} = 2.3$ in 22
Isotherm zone 70-75	$\bar{x} = 1.8$ in 8

In Tinkle's study, 15 northern (Connecticut, Illinois, Indiana, Kansas, Maryland, Michigan, New Jersey, New York, Pennsylvania) females had clutches averaging 4.6, whereas in 30 southern (Alabama, Arkansas, Florida, Georgia, Louisiana, Tennessee, Texas) females, eggs averaged 2.2 (1-4). However, the findings of later investigators do not conform well with this pattern.

Oklahoma, Arkansas $\bar{x} = 3.0$ (2-3) in 13
South Carolina, Savannah River $\bar{x} = 5.6$ in 25
Northeastern Alabama $\bar{x} = 3.2$ in 58
Central Alabama $\bar{x} = 2.7$ in 96
Florida $\bar{x} = 2.9$ in 17

As these records are concentrated in the southern one-third of the species range, they are not well suited to show latitudinal variation. Proof that clutch size increases northward, as believed by Tinkle, must await accumulation of substantial samples from the northern part of the range.

Terrapene carolina. Two substantial samples of clutches are available.

Northern (District of Columbia; sbsp. *carolina*) $\bar{x} = 4.2$ (2-7) in 60
Southern (Florida, Gulf and Franklin counties; sbsp. *major*) $\bar{x} = 2.7$ (2-5) in 36

Northward increase is strongly indicated. The Washington, D.C., sample was ob-

tained by Allard (1935) from clutches laid by penned females. His figures differed slightly from year to year as follows: 1932, $\bar{x} = 4.1$ (3-6) in 8 females; 1933, $\bar{x} = 4.5$ (3-7) in 17 females, and 1934, $\bar{x} = 4.1$ (2-6) in 35 females. Eggs were laid in June and July.

The southern sample, studied by Tucker et al. (1976) was obtained from 18 females with oviducal eggs and 18 with ripe follicles. A few females were estimated to produce as many as 5 clutches per season, 30% produced at least 4, 72% produced 3, and 92% produced 2. Northern box turtles, also, may produce more than one clutch, but they compensate for the shorter growing season and fewer clutches by increasing the number of eggs per clutch.

Trionyx muticus. Three samples are available to show clutch size in this highly aquatic turtle of the eastern and central United States.

Northern (Illinois, Iowa, Missouri)
$\bar{x} = 18.6$ (4-33) in 25
Central (Kansas) $\bar{x} = 10.6$ (3-23) in 124
Southern (Oklahoma, Texas)
$\bar{x} = 9.0$ (3-25) in 9

It is evident that clutch size increases northward. Accompanying changes from south to north are those characteristic of freshwater turtles in general: increased size of egg; fewer clutches (1 or 2 vs 3) per season; longer time lapse before attainment of sexual maturity.

Trionyx spiniferus. Scattered records from various parts of the range, summarized by Webb (1962), and series from Wisconsin (Vogt, Bull and McCoy, 1982), and Tennessee (Robinson and Murphy, 1978) seem to show a latitudinal trend in clutch size in this aquatic turtle.

Northern (Minnesota, Michigan, Indiana, Illinois, Nebraska)
$\bar{x} = 19.0$ (9-27) in 21
Northern (Wisconsin, Vernon County)
$\bar{x} = 15.3$ in 25
East-central (Tennessee)
$\bar{x} = 14.8$ (9-20) in 5
Southwestern (southern Oklahoma, Texas)
$\bar{x} = 9.6$ (3-17) in 17

Increase in clutch size northward is indicated. Turtles of this species have the capacity to produce several successive clutches annually, 4 or 5 at the latitude of Illinois, according to Moll (1979). Probably southern populations produce more clutches than northern populations, compensating, in part, for the smaller clutch size.

LIZARDS

The reproductive strategies of lizards are influenced by the fact that most are active, fast moving animals depending on speed and agility to capture prey and escape their enemies, that locomotion is usually quadrupedal or bipedal, resisting gravity, with eggs or embryos an added burden to the gravid female; that the sexes are usually unequal in size, with females larger *except* in those groups in which male rivalry and combat is prominent; that there are both egg-laying (primitive) and live-bearing (derived) kinds, but the former condition is much more common, and females usually produce multiple clutches annually. In two highly successful and varied tropical groups clutch size is constant (two eggs in geckonids except sphaerodactylines, which have only one, and one egg in anoline iguanids). These groups having fixed clutch size do not figure in the discussion below. Relative clutch mass (clutch weight divided by total weight of female parent) averages .224 for 93 species of lizards, with no significant difference between egg-layers and live-bearers (Vitt and Price, 1982). Compared with snakes, lizards in general have relatively small broods. As in other groups, variation in clutch or litter size seems to be closely correlated with size of female; populations in which adults average large (because of genetic constitution or favorable environment or a combination of the two) have relatively large clutches or litters.

Ameiva ameiva. This wide-ranging large teiid occurs in a variety of climates in Central and South America, and probably its clutch size varies in adaptation to local conditions.

Caatingas, northeastern Brazil
$\bar{x} = 5.6 \pm 0.2$ (1-9) in 80
Santa Cecilia, Amazonian Ecuador
$\bar{x} = 3.72$ (2-6) in 13

The caatingas are a semi-arid region of xeric scrub forest with a long dry season whereas the climate of Santa Cecilia is relatively aseasonal with moderate to high

precipitation throughout the year. Most egg production at Santa Cecilia seems to be limited to about half the year, July through December. There is some reproduction year-round in the caatingas, but with peaks during August-October (late dry season) and January-February (rainy season). It seems that females of both populations produce multiple clutches but probably those of Santa Cecilia produce the greater number.

Ameiva festiva. One large local sample and one small composite sample available for this tropical forest lizard seem to indicate geographic variation in clutch size.

Costa Rica, Caribbean lowlands, Pandora
$\bar{x} = 2.2$ in 87

Costa Rica, low to medium elevations (Cariblanco, Limon, Rio Pacuare, Tenorio, Turrialba)
$\bar{x} = 3.0 \pm 0.2$ (2-4) in 6

Except for Limon, the miscellaneous localities of the second sample were well above sea level, and in general they were in more seasonal climates than that of Pandora. Evidently the lizards respond to such change with a shorter breeding season and a larger clutch.

Ameiva undulata. This abundant teiid occurs over a considerable range of latitude, altitude and habitat. Probably clutch size changes in response to environmental factors, but records are few.

Pisté, Yucatan, Mexico, 20°45′N
$\bar{x} = 5.3 \pm 0.5$ (2-7) in 9

Nicaragua and Costa Rica, 9°-13°N
$\bar{x} = 3.3 \pm 0.5$ (1-5) in 8

Seemingly clutch size is larger in the more seasonal northern part of the range. Length of the breeding season varies according to locality, but corresponds with the wetter part of the year. Growth to sexual maturity can occur in as little as four months, allowing time for two generations in the course of a year.

Basiliscus basiliscus. Clutch size in the basilisk is known chiefly through the work of Van Devender (1982).

Rio Corabicí, Guanacaste, Costa Rica
$\bar{x} = 10.4$ (6-18) in 38

Rio Sandillal, Guanacaste, Costa Rica
$\bar{x} = 8.4$ (3-13) in 34

The Rio Sandillal is a tributary of the Corabicí and the two study areas are separated by only 8 km of continuous habitat, hence it is evident that gene flow can occur readily in either direction. However, habitat conditions are somewhat different; the Sandillal is small, sluggish and muddy, whereas the Corabicí is larger with a swift current and a rocky bed. Population densities, sex ratios, sexual dimorphism, survivorship, and number of clutches per year all differed notably between the two areas. Van Devender (1982) noted that broad geographic comparisons could be jeopardized by such local variations.

Basiliscus vittatus. This large semiaquatic lizard has an extensive range in the tropics, from equatorial regions to those with sharply seasonal climates. There is evidence of important variation in clutch size.

Chilpancingo, Guerrero, Mexico, 17°30′N
"6-8 eggs in large females;
4-5 eggs in smaller females"

Veracruz, Oaxaca, and Chiapas, Mexico, 16°-19°N $\bar{x} = 6.9 \pm 1.1$ (3-16) in 15

Northeastern Costa Rica, 10°-11°N
$\bar{x} = 3.9$ (2-6) in 40

In Costa Rica there is probably some breeding throughout the year, but it is at low ebb during November, December and January. An output of four clutches per breeding season seems a reasonable estimate, but on the conservative side. However, in the sharply seasonal climate of the Chilpancingo region the breeding season is relatively short, with perhaps only one clutch per season.

Callisaurus draconoides. Several samples are available to show clutch size in this common desert lizard. Evidence for geographic variation in this regard is entirely negative.

Range in general (11 localities, 28°-40°N)
$\bar{x} = 4.4$ (2-8) in 73

Mid-northern (southern Nevada, Test Site)
$\bar{x} = 4.5 \pm 0.2$ (3-6) in 14

Southern (lower Colorado River)
$\bar{x} = 4.6$ (1-8) in 34

Southeastern (southern Arizona)
$\bar{x} = 4.5$ (3-7) in 12

Normally this lizard matures within the first year, and it seems there are usually two clutches or more per season. Length of growing season and severity of winter vary greatly and must cause some changes in

reproductive strategies, but as yet these have not been demonstrated.

Cnemidophorus deppii. Small samples are available for comparison from the northern and southern parts of the range.

Northern (Mexico, Guerrero, Oaxaca, Morelos, Veracruz, 16°-19°N)
$\bar{x} = 2.7 \pm 0.2$ (2-4) in 13

Southern (southwestern Nicaragua, northwestern Costa Rica, 10°-12°N)
$\bar{x} = 3.0 \pm 0.3$ (1-4) in 11

Northward decrease is suggested. Reproduction is seasonal in both northern and southern populations. In the latter the long and severe dry season inhibits egg production.

Cnemidophorus gularis. In the vicinity of San Angelo, Texas, Ballinger and Schrank (1972) found an average of 4.5 eggs in 154 females. However, farther southwest in the more xeric climate of trans-Pecos Texas, Schall (1978) reported an average clutch of 3.1 (1-5) in 23.

Cnemidophorus inornatus. The several available samples of clutch size in this small, southwestern desert whiptail indicate both latitudinal and altitudinal change.

Albuquerque, New Mexico
$\bar{x} = 2.3$ (1-3) in 68

Central Arizona, 1600 to 2000 m
$\bar{x} = 3.3$ (2-5) in 26

Southwestern New Mexico $\bar{x} = 2.2$ in 16

Southwestern Texas $\bar{x} = 2.4$ (1-5) in 87

Central Chihuahua, Mexico
$\bar{x} = 2.2$ (1-3) in 17

Coahuila and Nuevo Leon, Mexico
$\bar{x} = 2.1$ (1-4) in 13

With the exception of the Arizona sample, these collections came from elevations of 1500 m or less. Sharply increased clutch size at high altitude is indicated, with less well defined increase from south to north. The high altitude Arizona population produces a single annual clutch, whereas others produce two or more. Body size was found to be greater in the high altitude Arizona population. Females were found to be relatively large in the most southern (Coahuila, Nuevo Leon) population, which however, produced relatively small eggs. Degree of sexual dimorphism varied markedly, with females slightly larger than males in some populations, and much smaller in others (Walker, 1981).

Cnemidophorus lemniscatus, C. ocellifer, and **C. arubensis.** These three large South American species are closely related. They are alike in having pronounced sexual dimorphism, with males larger than females. *C. lemniscatus* is widely distributed and occurs in a variety of habitats. It may continue its reproduction year-round in relatively aseasonal climates, but reproduction ceases or is much slowed where there are severe dry seasons. At Cumaná, Leon and Cova (1973) found a high level of egg production in April through September, but virtually none in the dry months, November through March.

Northeastern Brazil *(ocellifer)*
$\bar{x} = 2.7$ (1-5) in 58

Venezuela, Cumaná, xeric scrub *(lemniscatus)* $\bar{x} = 2.6$ (2-5) in 94

Guayana, Kartabo; Venezuela, Carapito, in evergreen forest *(lemniscatus)*
$\bar{x} = 2.0$ (2 in each of 5)

Aruba Island, Netherlands West Indies *(arubensis)* $\bar{x} = 1.0$ (1-2) in 38

Significantly the largest clutches occur in regions of severe dry season, caatinga and xeric scrub, where reproduction is limited to part of the annual cycle. Schall (1983) whose study revealed the one-egg clutch of *arubensis*, speculated that the explanation might be found in the largely herbivorous feeding of this species. A clutch averaging more than three eggs might be expected in a *Cnemidophorus* of this size according to Schall. However, a more plausible explanation of the reduced clutch is perhaps the effect of an insular environment, with relatively few natural enemies. The single egg of *arubensis* is relatively large.

Cnemidophorus parvisocius. This small Mexican whiptail of the *sexlineatus* group has a limited range in xeric habitats of Tomellin Canyon in southeastern Puebla and north-central Oaxaca. Walker (1981) was able to discern notable differences, chiefly in size, between northern and southern populations living at different altitudes and in somewhat different habitats. However, clutch size was found not to be significantly different.

Northern $\bar{x} = 1.75$ (1-3) in 40

Southern $\bar{x} = 1.8$ (1-4) in 45

Females of the Puebla population were found to average 57.4 (52-63) mm SVL, N = 72, whereas those of the Oaxaca popula-

tion averaged 60.3 (50-69), N = 101. Males were slightly larger than females in both populations. In both sexes maturity is attained in June of the year following hatching.

In contrast to the small clutch in the diminutive *C. parvisocius,* smallest member of the *sexlineatus* group, Walker (1970, 1981) found relatively large clutches in two closely related but much larger members of the *sexlineatus* group living at about the same latitude. In the sympatric *C. sacki,* clutch averaged 5.8 (3-10) N = 34 (mean SVL 127.2 mm in males, 111.9 in females). In *C. lineatissimus* of Michoacan (mean SVL 91.5 mm in males, 81.7 in females), clutch averaged 4.8 eggs (N = 14). In the large *C. communis* of Jalisco, Colima, and Michoacan clutch averaged 6.6 (N = 17).

Cnemidophorus sexlineatus. Many samples are available, but no clear-cut geographic pattern can be discerned.

Northeastern (North Carolina)
$\bar{x} = 3.0 \pm 0.8$ (1-5) in 67
Northwestern (Kansas, Missouri)
$\bar{x} = 3.2$ (1-8) in 79
West-central (northern Texas, Oklahoma)
$\bar{x} = 2.8$ (1-6) in 133
Central (Arkansas) $\bar{x} = 3.4$ (1-6) in 98
Southwestern (southeastern Texas)
$\bar{x} = 3.4$ (3-4) in 8
Southeastern (Alabama) $\bar{x} = 3.1$ (1-6) in 37

The above figures were obtained by combining a larger number of samples, and in some instances the two or more sets of figures available for a state or region were quite different, indicating that factors other than geographic variation have important influence on clutch size. Trauth (1983) whose figures provided the majority of records for the summary above, found that clutches average larger early in the season. Also, he found important differences in clutch size from year to year. For instance, in Arkansas he reported change in mean clutch from 3.4 in 1973 to 3.8 in 1975 to 3.0 in 1980 (a drought summer).

Cnemidophorus tigris. Many samples, some of them large, are available to show clutch size in this desert teiid (Fig. 2). *Cnemidophorus bacatus* and *C. martyris,* insular species of the Gulf of California, are included because they are closely related geographic representatives of *C. tigris* and demonstrate an extension of the trends in that species. The highest mean clutch size, 4.1, is from the San Gabriel Mountains in southern California at 1,585 to 1,830 m altitude, and in that area there are one or two clutches per season. Elsewhere, the higher means, 2.6 to 4.0, are from the northern half of the range, whereas the lower means, 1.3 to 2.5, are from the southern half. In the northern part of the range, Idaho, Colorado and the northern parts of Nevada and Utah, there is a single clutch, but in the southern part of the range there are two or more. Age at maturity is reduced in southern areas. In the small *C. martyris,* Walker (1980) found the entire population to be breeding adults in August, whereas in northern *C. tigris* first-year young and even second-year young are still immature in the breeding season. Pianka (1970) found that in one locality in the southern California desert, mean clutch increased from 2.3 in the dry year of 1963 to 3.4 in the relatively wet year of 1964.

Clutch size varies erratically and geographic trends are not consistent. In most instances, at least, clutch size is probably proportional to body size. In the southern part of its range *C. tigris* occurs sympatrically with at least nine of its congeners. Case (1983) has shown that through character displacement body size in *C. tigris* is much influenced by sympatric and competing species. In sympatry with the giant *C. burti, C. tigris* is relatively small, but with the diminutive *C. hyperythrus* it tends to be relatively large.

Cophosaurus texanus. The four samples available to show clutch size in this desert lizard indicate that there is notable geographic variation.

Eastern (northeastern Texas, Trinity River)
$\bar{x} = 5.0 \pm 0.01$ in 269
Central (Texas, near San Angelo)
$\bar{x} = 6.1 \pm 0.03$ in 244
Southwestern (Texas, Brewster County, Grapevine Hills) $\bar{x} = 3.1$ (2-5) in 25
Western (southern Arizona)
$\bar{x} = 3.6$ (2-7) in 31

There seems to be a reduction of clutch size in the relatively dry climate of the western part of the range. Also, there is seemingly a reduction in number of clutches, with three to six in central Texas, but only one to three in Brewster County.

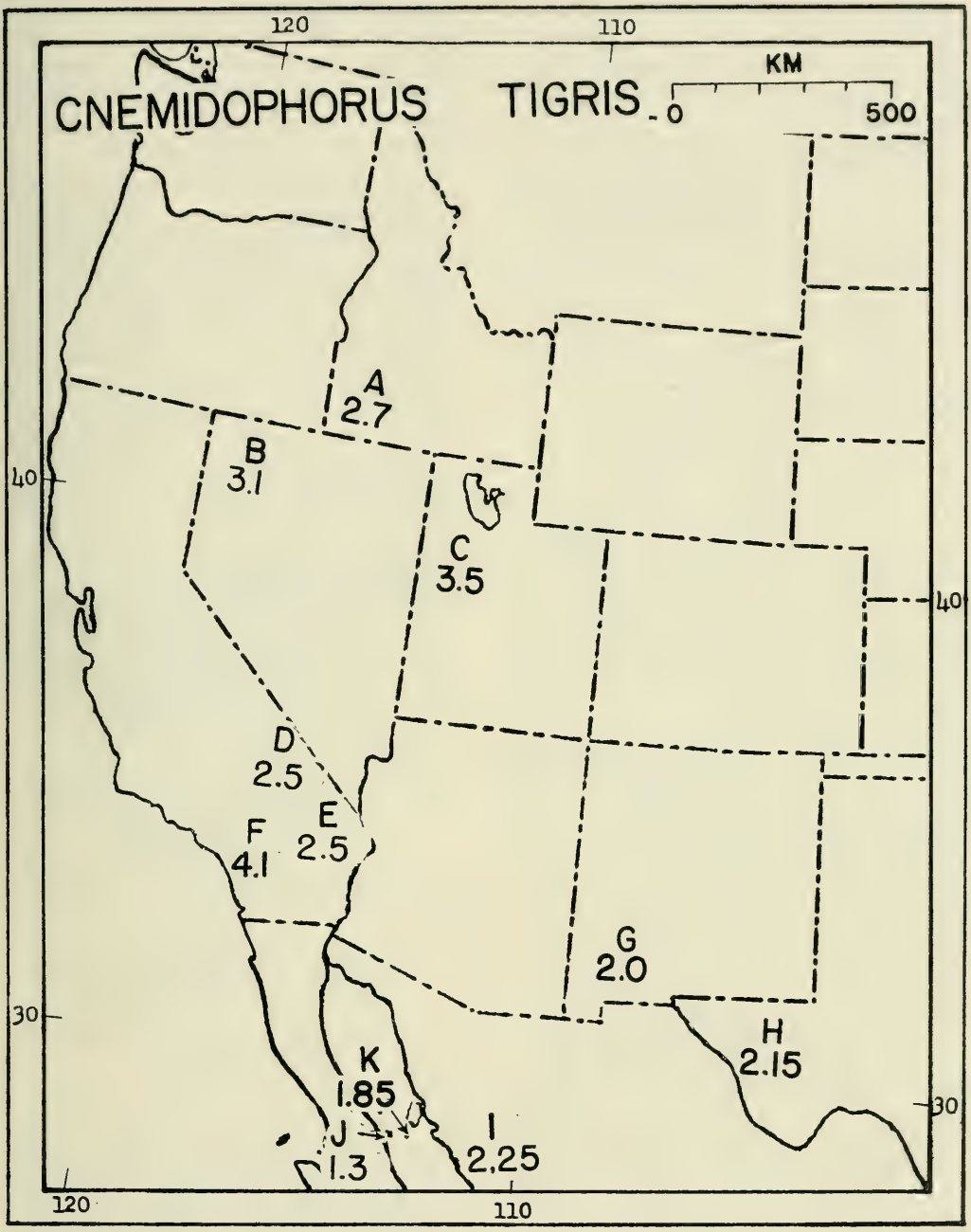

FIG. 2.—Map showing geographic variation in clutch size in *Cnemidophorus tigris* and satellite insular species. A. SW Idaho *(tigris)* **2.7** ±0.1 in 81; B. N Nevada *(tigris)* **3.1** ±0.2 in 12; C. Utah and W Colorado *(septentrionalis)* **3.5** in 60; D. S Nevada and Mohave Desert, California *(tigris)* **2.5** ±0.1 in 89; E. Colorado Desert, California and S Arizona *(gracilis)* **2.5** ±0.1 in 131; F. San Gabriel Mountains, SW California *(multiscutatus)* **4.1** in 56; G. S New Mexico *(gracilis)* **2.0** in 30; H. W Texas *(gracilis)* **2.15** in 176; I. Sonora and Sinaloa *(aethiops)* **2.25** ±0.1 in 16; J. Isla San Pedro Martir *(martyris)* **1.3** in 27; K. Isla San Pedro Nolasco *(bacatus)* **1.85** in 48.

Crotaphytus bicinctores. This far western species of collared lizard has on the average a smaller clutch than its near relative *C. collaris*. Thirteen clutches averaged 4.4, with some indication of latitudinal change when northern and southern groups were segregated.

Northern (southern Idaho; Millard and Tooele counties, Utah) 5.0 (3-8) in 6
Southern (Kane County, Utah; Clark County, Nevada; San Bernardino County, California) 3.9 (2-5) in 7

Northward increase is suggested by these small samples.

Crotaphytus collaris. The four substantial samples available span much of the geographic range but indicate only minor geographic variation in clutch size.

Northern (northeastern Kansas)
$\bar{x} = 6.9 \pm 0.3$ (2-11) in 86
East-central (Arkansas)
$\bar{x} = 6.5 \pm 0.2$ (3-11) in 99
Southern (western Texas)
$\bar{x} = 7.2 \pm 0.1$ in 88
Far southern (Mexico, Nuevo Leon)
$\bar{x} = 6.1 \pm 0.3$ in 36

In these four populations mean female SVL in millimeters was 95.2, 89.7, 86.3, and 91.9, respectively.

In western Texas Hipp (1977) found much variation in size of clutch from year to year, and clutch size was positively correlated with amount of winter precipitation. In northeastern Kansas (Fitch, 1970), I also found much variation from year to year, with reduced reproduction in years of heavy precipitation. In this area at the northeastern extreme of the range, food and moisture were abundant but rain and overcast could be limiting in drastically reducing time available for basking and foraging. Two small samples from the southwestern part of the range seem to indicate reduction in clutch size under xeric conditions there. Parker (1973) found 5.3 ± 0.35 (3-7) eggs in 11 in a mixed sample from western Texas, New Mexico, and southeastern Arizona, and Vitt (1977) found 5.6 (4-7) eggs in 5 from unspecified localities in Arizona, California and Nevada which might have included *C. bicinctores* material.

Elgaria coerulea. Seven samples are available to show litter size in this viviparous West Coast anguid (Fig. 3). Three montane populations all have larger litters than any of four coastal populations. Litters average largest in the population having the largest body size, that of Trinity County, California, but those from southern Oregon and Eldorado County, California, have smaller litters than the Trinity County lizards, even though they live at higher altitudes.

Stewart (1979) studied relationships between number of young per litter, female size, and clutch size in the three California populations (E, F, and G on the map). He found clutch size positively correlated with female size, with an inverse correlation between newborn size and litter size. Over the range as a whole, the pattern seems to be one of increased litter size in montane populations; on the coast litter size increased somewhat both to the north and to the south, compared with centrally located populations.

Elgaria multicarinata. The several available samples of this West Coast anguid seem to show clinal decrease in clutch size northward, and also show an abrupt decrease from the mainland population of southern California to that of Los Coronados Islands offshore at nearly the same latitude.

Northern (Oregon, sbsp. *scincicauda*)
$\bar{x} = 9.9 \pm 0.4$ (8-14) in 11
Central (northern California, Sacramento Valley; sbsp. *multicarinatus*)
$\bar{x} = 10.8 \pm 0.8$ (9-17) in 16
Southern (Kern and Los Angeles counties, California; sbsp. *webbi*)
$\bar{x} = 12.2$ (8-17) in 16
Southernmost (San Diego and Riverside counties, California; sbsp. *webbi*)
$\bar{x} = 12.8$ (5-41) in 40
Southern insular (Los Coronados Islands, Mexico; sbsp. *nanus*)
$\bar{x} = 8.8$ (1-18) in 30

In the northern part of its range *(scincicauda)*, the species is single-brooded, whereas at the latitude of southern California, both mainland *webbi* and insular *nanus* are known to produce two clutches (Burrage, 1965). Body size decreases slightly from south (136 mm SVL in San Diego County) to north (130 mm SVL in Oregon). Also, relative size of the female increases, from 93.1 per cent of male length in San Diego County to 97.5 per cent in Oregon.

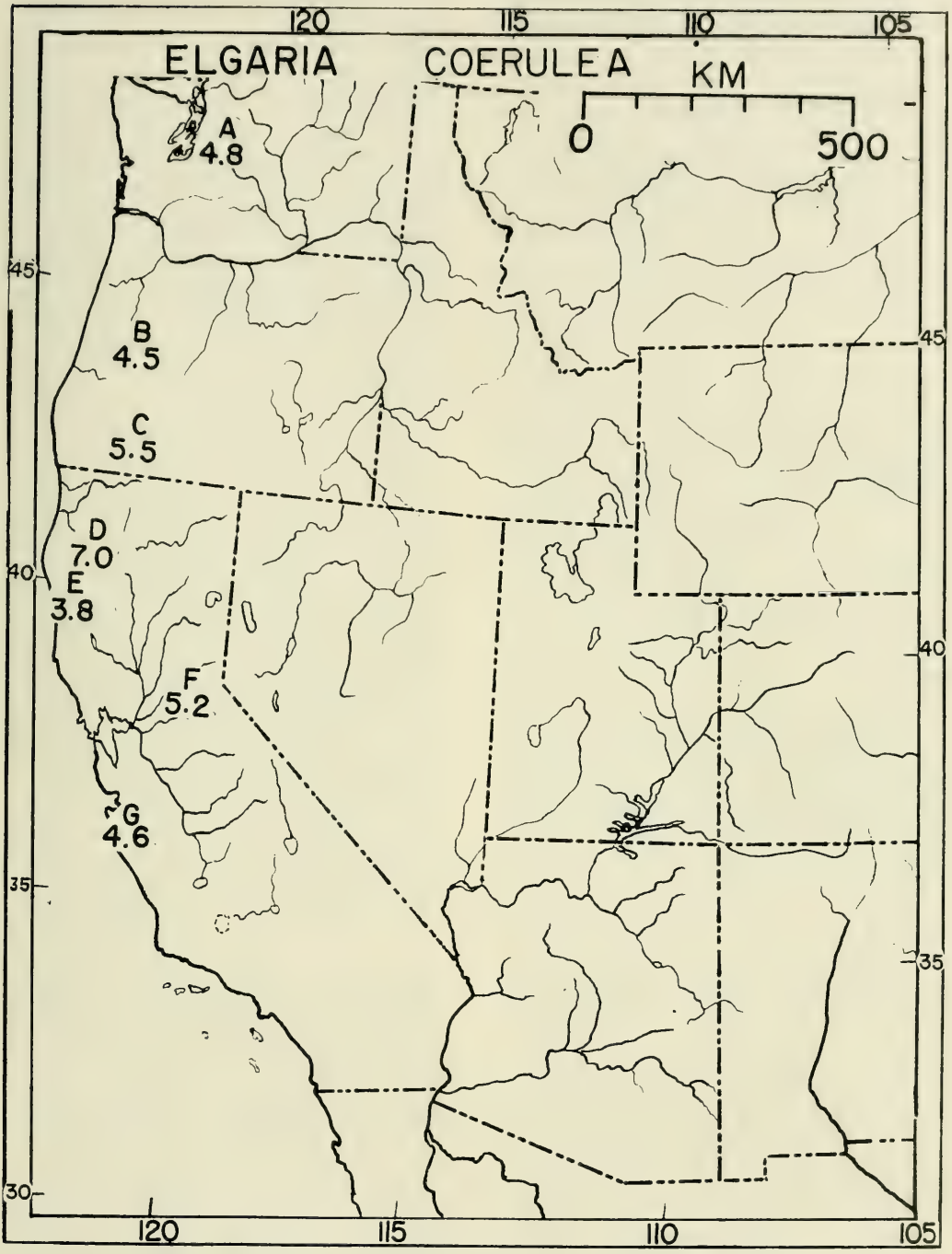

FIG. 3.—Map showing geographic variation in litter size in *Elgaria coerulea*. A. W Washington *(principis)* **4.8** in 20; B. W-central Oregon in Lane and Douglas cos. *(principis)* **4.5** ±0.25 (2-6) in 14; C. S Oregon, montane, above 1500 m *(principis-shastensis* intergrades) **5.5** ±0.5 (2-8) in 10; D. NW California, inland, Trinity County *(shastensis)* **7.0** ±0.4 (6-9) in 7; E. NW California, coastal, Mendocino County *(principis)* **3.8** ±0.2 (2-7) in 71; F. E California, Eldorado County, 1400 m *(palmeri)* **5.2** ±0.2 (3-9) in 54; G. California, central coast, Monterey County *(coerulea)* **4.6** ±0.2 (3-9) in 40.

Eumeces fasciatus. Several local series and isolated records have been combined for 6 geographic samples of clutch size of this common skink.

Northernmost (Michigan)
$\bar{x} = 9.4 \pm 1.00$ (6-14) in 8
North-central (Ohio, Indiana, Kentucky)
$\bar{x} = 8.6$ (5-12) in 42
Northwestern (northeastern Kansas)
$\bar{x} = 9.2$ (4-15) in 64
West-central (Oklahoma, Arkansas)
$\bar{x} = 8.4$ (6-10) in 6
East-central (Virginia, North Carolina)
$\bar{x} = 7.6$ (6-11) in 5
Southeastern (South Carolina)
$\bar{x} = 7.0$ (4-10) in 6

The figures provide meager evidence of southward reduction in clutch size. A few additional scattered records are available from the southern part of the range (Reynolds, 1958). In some of the southern records egg counts are relatively high, 13 to 20. However, a few of these may have belonged to the large sympatric *Eumeces laticeps* not easily distinguishable in the field; others may have been combined clutches of two or more females, as communal nesting is known to occur.

Eumeces obsoletus. Simbotwe (1978) studied geographic variation in clutch size in 132 females of this large grassland skink. Separating the northern population, north of latitude 37°N from those south of this line, he reported substantial differences as follows:

Northern $\bar{x} = 15.15 \pm 1.6$ (8-32)
Southern $\bar{x} = 10.9 \pm 0.8$ (5-20)

Hall and Fitch (1972) found a mean of 12.3 ± 0.5 (7-24) eggs in 37 females from northeastern Kansas, mainly from Douglas and Jefferson counties, at about 39°N. Throughout its range this species produces a single annual clutch. In the more northern populations some females mature as three-year-olds, others a year later. Time to maturity may be shortened in southern populations, but as yet evidence for this is lacking.

Eumeces septentrionalis. One medium-sized local sample and one small mixed sample give some indication of clutch size and its geographic variation in this grassland skink.

Northern (Minnesota)
$\bar{x} = 8.8 \pm 0.55$ (5-13) in 19
Central-southern (Nebraska, Kansas, Texas) $\bar{x} = 11.7 \pm 1.0$ (6-18) in 12

Increase in clutch size southward is suggested. Like other *Eumeces* species, this one produces a single clutch annually, as the female remains with her eggs throughout several weeks of incubation. There may be a reduction of time from hatching to maturity, from three years in the northern part of the range to two years in the southern part, with resulting increased reproductive potential.

Eumeces skiltonianus. Available samples are small and not adequate for convincing evidence of geographic variation in clutch size.

Northwestern Utah
$\bar{x} = 4.2 \pm 0.2$ (2-6) in 19
San Bernardino County, California
$\bar{x} = 4.7$ in 6

Van Denburgh (1922) found 5 eggs in a Monterey, California, female, and Stebbins (1954) found 8 to 9 eggs in 8 California clutches, suggesting the possibility that clutch size is greater on the West Coast than in the Great Basin, and increases northward in the coastal region.

Gambelia wislizenii. Many records with several substantial series are available to show geographic variation in clutch size in this predatory desert iguanid.

Northern (Idaho, northern Nevada, northern Utah) $\bar{x} = 5.3$ in 85
Eastern (western Colorado) $\bar{x} = 7.3$ in 10
South-central (Mojave Desert, California; southern Nevada) $\bar{x} = 6.1$ in 43
Southwestern (southern California)
$\bar{x} = 5.2$ in 14

The records do not clearly indicate latitudinal trends, but clutches tend to be larger in the southern half of the range. Sixteen northern clutches (north of 37°N) averaged 4.94, whereas 47 more southern clutches averaged 6.05. Females normally mature late in their second year, but some individuals of some (southern) populations mature at an age of 9 months, and so are able to produce eggs in the year following that in which they hatch. Females average larger than males (111.5 mm SVL, N = 90, vs 104.6 mm, N = 91; Tollestrup, 1982). One clutch per year is the normal complement, but under favorable circumstances, in some years and some localities, a second clutch may be produced.

In the closely related *Gambelia silus* of California's San Joaquin Valley the clutch averages only 2.9 eggs, with no variation between three study sites according to Tollestrup (1982). However, females of *G. silus* normally mature in their first year.

Holbrookia maculata. Data for this species (Table 1) are based on an examination of 460 museum specimens with 115 clutches (KU and MVZ) from Nebraska, Kansas, New Mexico, Arizona, Sonora, Chihuahua and Coahuila, supplemented by 80 clutches mentioned in published literature (Gehlbach and Collette, 1959; Parker, 1973; Vitt, 1977; Werth, 1972; Droge, Jones and Ballinger, 1982, and Gennaro, 1974). Several parallel clines are evident. Number of eggs per clutch increases southward and is nearly doubled from Nebraska to Arizona, New Mexico, and adjacent Mexico. Likewise, there is increase in body size from north to south, so that southern females are approximately twice the bulk of their northern counterparts. A third latitudinal trend is from relatively large females (exceeding male size by several per cent) in Nebraska and Kansas, to relatively small females (several per cent smaller than males) in Arizona, New Mexico, and adjacent Mexico.

Holbrookia propinqua. Substantial samples are available for comparing the insular population of Padre Island to that of the adjacent mainland of southern Texas through the study made by Judd and Ross (1978).

Texas mainland $\bar{x} = 4.5$ (3-7) in 69
Padre Island, Texas coast
$\bar{x} = 3.2$ (2-4) in 123

Clutch size averaged larger on the mainland even though females there averaged slightly smaller, 48.8 mm SVL vs 50.3 in the island population. Both populations were found to have a long breeding season, with production of several successive clutches. However, on the mainland females produced about one more clutch, on the average, than did those on the island. Clutch size varied much more from year to year on the mainland than on the island, seemingly in response to varying amounts of rainfall. The authors attributed the lower clutch size in the island population to relatively low predation compared with that affecting the mainland population.

Iguana iguana. This giant herbivorous lizard ranges throughout the New World tropics in a wide variety of climates and habitats. Probably there is much geographic variation in clutch size, but as yet relatively little information is available.

Western Nicaragua, 12°N
$\bar{x} = 30.5 \pm 2.1$ (11-54) in 31
Northeastern Costa Rica, 10°30′N
$\bar{x} = 35.3 \pm 1.3$ (29-40) in 7
Central Panama, 9°N
$\bar{x} = 40.6$ (9-71) in 30
Curaçao, Netherlands West Indies, 12° 10′N $\bar{x} = 17.0 \pm 1.1$ (10-31) in 23

In the Panamanian females having the largest average clutch size, body size also averaged greatest (SVL 354 vs 324 for Nicaraguan females and only 262 for those from Curaçao). However, Rand (1984), comparing females of the same length in the populations of Panama and Nicaragua, found that the latter weigh less and produce smaller and lighter eggs. In each population there is a direct relationship between size of females and number of eggs in a clutch.

TABLE 1. Geographic variation in reproductive parameters of *Holbrookia maculata**

Area	Subspecies	Clutch Size		Egg Size (mm)	♀ Length S-V (mm)	Ratio ♀ to ♂ Length (%)
Nebraska	*maculata*	3.68	(1-7) in 55	11.1×?	47.3 in 12	103.5
Kansas	*maculata*	5.15	(2-9) in 72	10.2×6.3	51.9 in 47	104.9
Arizona-New Mexico	*approximans*	7.94	(2-10) in 43	11.2×7.2	53.0 in 73	98.9
Texas	*approximans*	6.10		11.7		
Sonora-Chihuahua	*approximans-thermophila*	6.14	(4-9) in 24		56.1 in 77	92.5

* Sources: Literature records from Droge, Jones and Ballinger (1982) for Nebraska and Texas; from Gehlbach and Collette (1959) for Nebraska; from Werth (1972) for Kansas; from Gennaro (1974) for New Mexico; from Parker (1973b) and Vitt (1977) for Arizona, with additional records from museum specimens examined by the author from Nebraska, Kansas, Arizona, New Mexico and Mexico.

Newly matured females produce relatively few eggs in their first clutches, whereas the maximum sized clutches are produced by old and large females. The small body size and small clutch on Curaçao conform with a trend that is typical of insular populations in many species of reptiles. Clutches of the endemic insular species, *I. delicatissima* from Ile Fourchue, Antigua and Dominica, had 17, 18, and 25 eggs respectively, indicating that its clutches are smaller than those of mainland *I. iguana*.

Mabuya caissara. This viviparous skink inhabits the mainland and adjacent small islands along the coast of São Paulo, Brazil.

Mainland (Ubatuba, Caraguatatuba, Bertioga) $\bar{x} = 4.8$ (2-9) in 46
Insular (São Sebastião) $\bar{x} = 3.8$ (2-6) in 8

The island of São Sebastião is only 2 km offshore, and its separation from the mainland seems to have occurred relatively recently in post-Pleistocene time, according to Vanzolini and Rebouças-Spieker (1976), who have studied the taxonomy and ecology of this skink and the closely related *M. macrorhyncha*. Body size is slightly smaller in the sample of São Sebastião females, 55-81mm SVL vs 62-87 in mainland samples. From the island of Ilhabela a sample of only two litters was available, but these had, respectively, 6 and 9 young, indicating the possibility of larger litter size, compared with either São Sebastião or the mainland. The Ilhabela females were found to be larger than those of other samples, 79-90 mm, SVL.

Mabuya mabouya, M. alliacea, M. brachypoda, M. unimarginata and **M. heathi.** The taxonomy of *M. mabouya* and its near relatives in Central and South America is still not well understood. Perhaps most of them are subspecies of *M. mabouya,* but are listed below as species. They are viviparous, and occur over a wide range of climatic conditions. There is evidence of geographic variation in litter size.

Mexico, Guerrero, Chilpancingo, 17°-18°N *(brachypoda)* "2, 3, and 4 embryos" (Davis and Dixon, 1961)
Southern Mexico *(brachypoda)* 4-6 embryos in 10
Mexico, Chiapas, 15°-18°N *(brachypoda)* "4-7 per litter" (Alvarez del Toro, 1960)
Costa Rica, 10°N *(unimarginata)* $\bar{x} = 5.15$ (2-7) in 7
Panama, Darien, 5°N *(mabouya)* $\bar{x} = 4.20$ (3-5) in 5
Amazonian Ecuador, 0°N *(mabouya)* $\bar{x} = 5.20$ (4-6) in 10
Brazil, Pernambuco, 7°36′S *(heathi)* $\bar{x} = 5.03 \pm 0.12$ (2-9) in 131

Three from eastern and southern Costa Rica *(alliacea)* in relatively humid, aseasonal climates had small litters of only 2, 2, and 1. One litter per year per female may be the usual rule. In the sharply seasonal climate of southern Mexico, Webb (1958) and Davis and Dixon (1961) found births concentrated in late June and early August, but in Costa Rica full term embryos were observed in March and August, and in Ecuador Duellman's (1978) records suggest acyclic breeding.

Mabuya macrorhyncha. This viviparous skink inhabits the mainland and adjacent small islands along the coast of southern Brazil, but is allopatric to its near relative, *M. caissara* of the same region. Vanzolini and Rebouças-Spieker (1976) who have studied these skinks, consider *M. macrorhyncha* to be the ancestral form and *M. caissara* to be a recently derived offshoot. *M. macrorhyncha* has smaller litters, and also differs from *M. caissara* in that females seemingly do not produce young until their second year. Hence its reproductive potential is substantially lower, but is subject to geographic variation.

Mainland (Enseada, Mongagua, Peruibe) $\bar{x} = 2.8$ (1-6) in 23
Insular (Vitoria) $\bar{x} = 3.6$ (2-5) in 5
Insular (Buizos) $\bar{x} = 3.3$ (2-4) in 35
Insular (Alcatrazes) $\bar{x} = 2.3$ (2-3) in 3
Insular (Queimada Grande) $\bar{x} = 2.3$ (2-4) in 46

Increased litter size on the islands of Vitoria and Buizos represents a reversal of the usual trend for litter size to decrease in insular populations. Adults on these islands are not detectably larger than their mainland relatives.

Ophisaurus attenuatus. Geographic variation in clutch size in the slender glass lizard may occur, but if so differences are small.

Northeastern Kansas $\bar{x} = 9.83 \pm 1.19$ (5-17) in 42

Arkansas, Alabama, Oklahoma
$\bar{x} = 10.5$ (5-16) in 11

The female produces only a single clutch per season, and guards her eggs until hatching. Seemingly sexual maturity is attained at a smaller size and earlier age in the Arkansas population than in the population of northeastern Kansas.

Phrynosoma cornutum. This oviparous desert lizard is notable for its large egg clutches, and seemingly it produces only one clutch per season according to Ballinger (1974). Mainly through the efforts of this author and of Howard (1974) several large series are available, representing much of the geographic range.

Northern (central northern and eastern Texas) $\bar{x} = 23.1$ in 41
Southern (southern and southwestern Texas) $\bar{x} = 23.0$ in 19
Western (western Texas, New Mexico, Arizona, Sonora) $\bar{x} = 29.2$ in 70

The northern and southern samples are similar, but clutch size is markedly increased in the western sample.

Phrynosoma douglassi. There are few samples of litter size in this viviparous montane lizard, except in the southern part of its range. To obtain a "northern" sample, scattered records from Utah, northwestern New Mexico, and one each from Oregon and northern Arizona, had to be combined. A distinct trend toward reduced litter size in the north is indicated. Nussbaum et al. (1983) noted that in the high Cascades a normal brood is only five.

Northern (Oregon, Utah, northern Arizona, northern New Mexico)
$\bar{x} = 11.4 \pm 1.1$ (6-21) in 16
Southern (southern Arizona, southern New Mexico, Sonora, Chihuahua)
$\bar{x} = 21.8$ (9-48) in 50

Phrynosoma platyrhinos. Howard (1974) found a mean of 5.6 ± 0.3 (2-10) eggs in 37 of these lizards from near Yuma, Arizona, 32°N. At the Nevada Test Site, 37°N, Tanner and Krogh (1973) found a mean of 6.7 (3-9) in 24 females, Pianka and Parker (1975) found a mean of 8.4 ± 0.4 (2-16) eggs in 46 females from scattered localities throughout the range, and Vitt (1977) found an average of 7.8 (6-10) in 6 females. Presumably the studies by Pianka and Parker, and Vitt included many records from farther north than those obtained by Tanner and Krogh. Thus, there is some evidence of increased clutch size from south to north. These lizards attain sexual maturity in the second year. Two clutches per year are normal in the southern part of the range, and may occur also in the northern part, but according to Pianka and Parker (1975) may be prevented by unfavorable weather in some seasons.

Sauromalus obesus. Two geographic samples are available to indicate clutch size in the chuckwalla.

California, San Bernardino County, Argus Mountains (sbsp. *obesus*)
$\bar{x} = 7.8$ (6-13) in 22
Arizona, Pima County, Ajo and Why Mountains (sbsp. *tumidus*)
$\bar{x} = 8.0$ (6-10) in 7

The reproduction of this herbivorous desert lizard is still poorly known. Hatchlings are never abundant, and the low incidence of gravid females in early summer suggests that individuals may produce only in alternate years or even less frequently. In years when rainfall is deficient, so that plant food is scarce and of poor quality, there may be no reproduction at all.

Two other species of chuckwallas, of giant size, and endemic to islands in the Gulf of California, *S. hispidus* and *S. varius*, have even lower rates of recruitment than *S. obesus*, judging from the usual scarcity of both gravid females and juveniles. However, both have relatively large egg clutches, as shown by Case (1982).

S. hispidus $\bar{x} = 22.0$ (14-24) in 4
S. varius $\bar{x} = 23.4$ (16-32) in 5

Perhaps their strategy is to concentrate production of young when a favorable weather sequence has promoted growth of succulent vegetation, serving as an ample food supply for females during vitellogenesis and juveniles during their early weeks of life.

Sceloporus aeneus. This small montane Mexican iguanid is remarkable for its reproductive bimodality. *S. a. aeneus* in the western part of the range is oviparous, whereas *S. a. bicanthalis* occurring farther east in the same mountain range is viviparous. The species' biology has been studied by Guillette (1982). *S. a. aeneus* mates in April, May and June, ovulates a few weeks later, and the young hatch from July through

September. *S. a. bicanthalis* mates in January and February, and the young are born in spring. The eggs ovulated by *S. a. bicanthalis* are much more bulky than those of *aeneus*.

Michoacan, Morelos, Mexico, D. F. (sbsp. *aeneus*) $\bar{x} = 5.6 \pm 0.4$ in 9

Veracruz, Mexico (sbsp. *bicanthalis*) $\bar{x} = 6.8$ in 4

Sceloporus clarki. The few available records of clutch size in this lizard suggest latitudinal change.

Northern (southern Arizona, sbsp. *clarki*) $\bar{x} = 15.2$ (8-24) in 17

Southern (Mexico; Chihuahua, Durango, Sinaloa; sbsp. *boulengeri*) $\bar{x} = 8.0 \pm 1.0$ (1-10) in 6

Sceloporus cyanogenys. The two series available suggest geographic variation.

Texas and Mexico $\bar{x} = 17.7$ in 25

Rio Grande, southern Texas $\bar{x} = 13.6$ (6-18) in 11

Whether latitudinal change accounts for the difference between these samples is uncertain. The first sample (from Crisp, 1964) may represent, on the average, more northern localities.

Sceloporus graciosus. The several available samples of this western lizard show notable geographic variation in clutch size (Fig. 4). Most means are between 3.5 and 4.5. The highest means, of 6.03 and 6.30 are, respectively, from the Wasatch Mountains of north-central Utah and from the Greenhorn Mountains in the southern Sierra Nevada of California. The lowest means are in the northwestern part of the range. The only samples showing the effect of altitude are those from southwestern Oregon, means 2.40 ± 0.27 (1-3) in 10 and 3.09 ± 0.22 (2-6) in 23 for lowland and montane samples, respectively. Body size varies and is greatest (63 mm SVL) in the Greenhorn Mountain population that produced the largest clutches, least (51.5 mm) in the population of southwestern Oregon that produced the smallest clutches. In northern populations the sexes are about the same size or, more frequently, the females are a little larger. On the contrary, in southern populations (Riverside County, California; Baja California) males are larger than females. Northern and high montane populations are single-brooded, but those occurring where there is a longer growing season, as in the southern part of the range, are believed to produce two clutches annually (Tinkle, 1973). These lizards normally mature late in the second year; however, depending on the locality, some females do not mature until the third year, and this is a further constraint on the reproductive potential in far northern or high montane areas where the season of activity is shortened.

Sceloporus grammicus. Three litter samples of this viviparous Mexican lizard are available from widely separated areas, and these show significant differences of several sorts.

Michilia Reserve, Durango, 26°N, 2,480 m $\bar{x} = 6.2 \pm 1.65$ (3-9) in 46

Las Vigas, Veracruz, 19°47′N, 2,300 m $\bar{x} = 5.7$ (4-7) in 7

Zoquiapan, D. F., 19°41′N 2,000-3,000 m $\bar{x} = 5.2 \pm 0.25$ (3-7) in 39

In Durango courtship and mating seemingly occur in late November and early December, and there is a gestation period of approximately six months with no embryonic diapause. In contrast, at Zoquiapan courtship and mating occur in September, and there is a two-month diapause, with births in May and June. Veracruz females have a different seasonal schedule with births in February or early March (average date 18 February).

Sceloporus jarrovi. The extensive range of this montane, viviparous iguanid is mainly within Mexico. Most available samples are from a limited area in southeastern Arizona, and these are of interest in demonstrating the effect of altitude, rather than latitude, on litter size. Ballinger (1979) compared populations in the Chiricahua Mountains and obtained the following figures for litter size at two altitudes:

Lower (1,675 m) $\bar{x} = 7.1 \pm 0.3$ (2-15) in 154

Higher (2,542 m) $\bar{x} = 8.4 \pm 0.3$ (3-16) in 106

As in most reptiles, size of brood is proportional to size of female, and reproductive females average larger at the higher altitude because only those two years old or older are mature. At the lower altitude first-year females mature, and their individually small egg complements make up a relatively large part of the total production. Even if

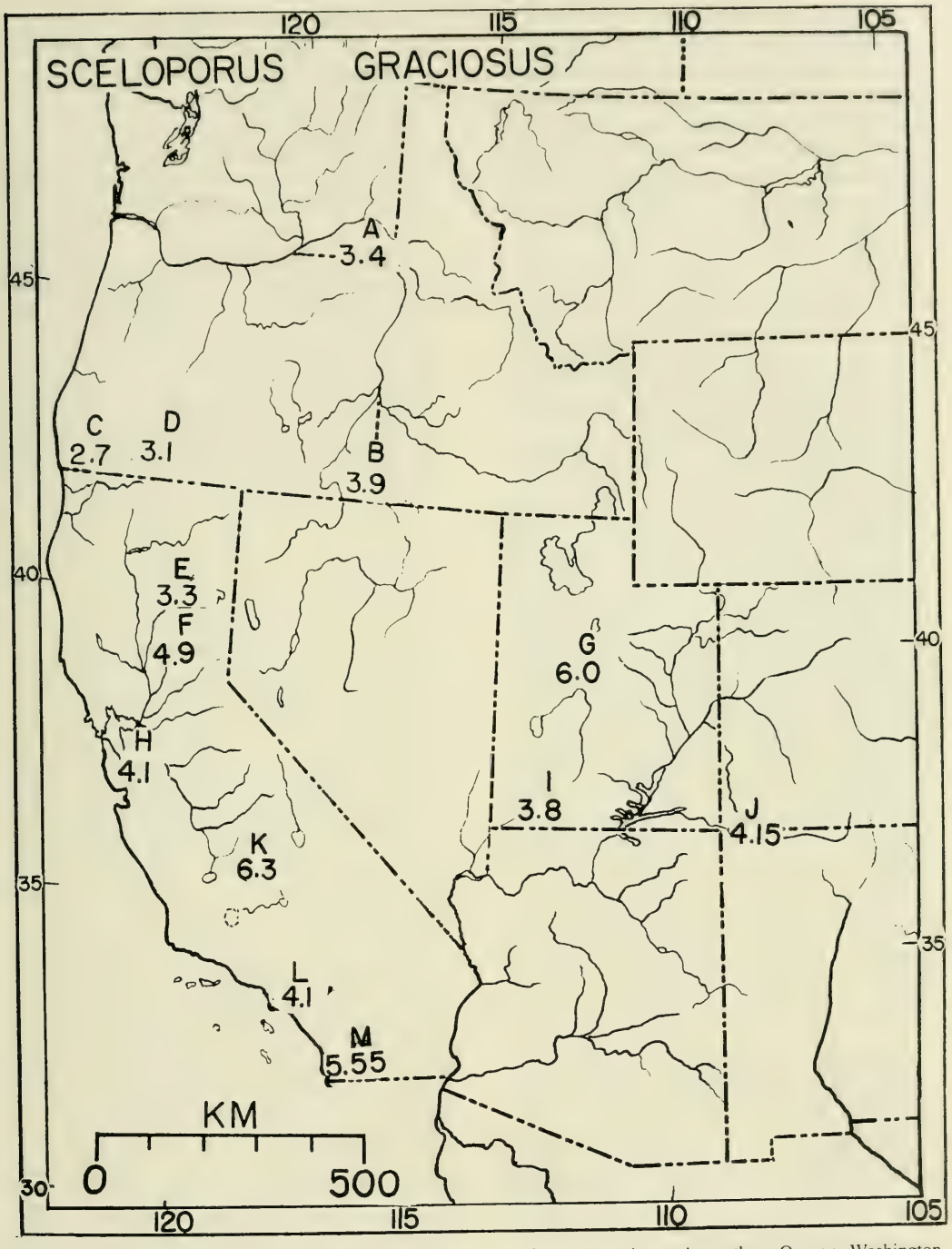

FIG. 4.—Map showing geographic variation in clutch size in *Sceloporus graciosus*. A. northern Oregon, Washington and Idaho **3.4** ±0.2 (3-5) in 15; B. southeastern Oregon, northern Nevada and Modoc County, California **3.9** ±0.4 (1-5) in 11; C. southwestern Oregon and Siskiyou County, California, lowlands, **2.7** ±0.3 (1-3) in 9; D. southwestern Oregon, montane, **3.1** ±0.2 (2-6) in 22; E. Mount Lassen region, California **3.3** (2-5) in 12; F. California, N Sierra Nevada, Placer and Nevada counties **4.9** in 78; G. central Utah, Spanish Forks **6.0** (2-10) in 143; H. central California, Mount Diablo **4.1** in ?; I. SW Utah, Zion Nat'l Park **3.80** in 72; J. SW Colorado, Mesa Verde Nat'l Park **4.15** (3-6) in 7; K. California, Kern County S Sierra Nevada **6.3** ±0.4 (4-8) in 10; L. San Gabriel Mountains, S California **4.1** in 78; M. SW California in San Bernardino, Riverside and San Diego cos. and Baja California del Norte **5.55** in 29.

transferred to lower elevation, with abundant food and relatively mild climate, the high montane females lacked the capacity to mature in their first year, but they outstripped their lowland counterparts in growth in experiments by Ballinger (1979). Two other samples of litter size, from different mountain ranges, are available.

Graham Mountains, 1,500-2,500 m (Tinkle and Hadley, 1973)
$\bar{x} = 6.75 \pm 0.3$ (2-11) in 52

Baboquiviri Mountains, 2,020 m (Goldberg, 1971) $\bar{x} = 6.7$ (2-12) in 85

In Morelos, Mexico, in the southern part of the range, Davis and Smith (1953) found an average of only 5 eggs (N = 8) suggesting a reduction in clutch size southward.

Sceloporus magister. In this oviparous, scansorial desert lizard there seems to be an increase in clutch size from north to south. Combining two northern samples, Tinkle (1976) for Washington County, Utah, and Tanner and Krogh (1973) for the Nevada Test Site, both about 37°N, and three southern samples, Shaw (1952) for Baja California and San Diego County, California, Vitt and Ohmart (1974) for the lower Colorado River region, and Parker and Pianka (1973) for southern California and Baja California between 29° and 35°N, yielded the following figures:

Northern $\bar{x} = 6.3$ (2-9) in 28
Southern $\bar{x} = 9.7$ (7-18) in 22

Some females mature as two-year-olds and others as three-year-olds. In some populations there is a single annual clutch; in others two clutches or even more may be produced. Doubtless these reproductive parameters are closely correlated with clutch size.

Sceloporus malachiticus. This montane tropical lizard occurs from southern Mexico south into Panama, but its populations are discontinuous, and well differentiated in some instances. In Costa Rica the lower edge of the range is at about 1,100 m, but farther north it descends to much lower elevations.

Guatemala, mostly below 1000 m (sbsp. *smaragdinus*)
$\bar{x} = 4.2 \pm 0.3$ (3-6) in 10

Costa Rica, 1,100-3,000 m (sbsp. *malachiticus*) $\bar{x} = 6.0 \pm 0.3$ (3-10) in 44

Sceloporus merriami. Although confined to a relatively small area in the Rio Grande region of Texas and northeastern Mexico, the canyon lizard may be subject to some geographic variation in clutch size.

Grapevine Hills, Big Bend National Park, Brewster County, Texas
$\bar{x} = 4.5 \pm 0.03$ (3-7) $N > 100$

Crockett County, western Texas
$\bar{x} = 3.7 \pm 0.1$ (2-5) in 27

Dunham (1981) studied *S. merriami* and *Urosaurus ornatus* in the Grapevine Hills area, and found many parallels in the life histories and ecology of the two. In *S. merriami* there were typically two clutches per season. As in most reptiles, clutch size was proportional to size of female, and body size averaged larger in "good" years of high precipitation than in dry years. Females of 50 mm SVL averaged 4.5 eggs per clutch in a wet year vs 4.0 eggs in a dry year. For smaller females, of 45 mm, the corresponding clutch sizes were 3.9 and 3.2. "Age-specific survival, age-specific fecundity, age-specific body size and growth rate, individual foraging success, and prehibernation lipid levels and body weights were all shown to vary significantly, both seasonally and among years, in both species." The Crockett County sample represents a single season, which may have been poorer than average resulting in the relatively small clutch. Also, geographic differences may be involved. The Crocket County sample came from a little farther north than that of the Grapevine Hills, but the latter probably represents, on the average, a higher altitude.

Sceloporus occidentalis. Many samples of clutch size are available for this common and widespread lizard of the western United States (Fig. 5). Mean clutch size varies from 6.5 to 13.4 eggs, but most sample means vary between 7 and 9. The highest means are all from high altitude series. Table 2 shows increase in clutch from relatively low areas to adjacent montane areas in 7 instances and suggests an average increase of one egg for 250 m of altitude. The main trends over the range seem to be from large clutches in the northern Sierra Nevada and Great Basin to small clutches in southwestern California and Baja California.

Northern and montane populations have the following characteristics correlated with

large clutch size: (1) there is a single clutch annually, (2) females are markedly larger than males, (3) body size is small. Conversely, the southern populations that produce relatively small clutches have up to three clutches annually, have males markedly larger than females, and have relatively large body size. In the large sample from Mendocino County, northern California, Schall (1983) found the mean clutch to be 9.35 (6-12) eggs in 34 females infected with malaria, vs 10.6 (6-14) in 119 unparasitized.

Sceloporus poinsetti. Samples from near the eastern and western extremes of the range have similar means, slightly higher than that in a small sample from farther south. Ballinger (1978), who gathered most of these records, found significant year-to-year differences in the means for New Mexico litters as follows: 10.8 in 1972–73; 8.3 in 1973–74; 12.5 in 1974–75.

Eastern (Texas, Irion County near Mertzon) $\bar{x} = 10.5 \pm 1.0$ (5-23) in 40

Western (southwestern New Mexico, Hidalgo County) $\bar{x} = 10.8 \pm 0.6$ (4-15) in 34

Southern (western Texas; Mexico, Chihuahua) $\bar{x} = 12.2$ in 10

Sceloporus scalaris. Two series of this small, widely ranging, montane lizard are available.

Southeastern Arizona, Chiricahua Mountains, 2600 m (sbsp. *slevini*) $\bar{x} = 8.5 \pm 0.2$ (3-14) in 153

Michoacan, 2100 m and lower (sbsp. *scalaris*) $\bar{x} = 6.9 \pm 0.4$ (4-9) in 12

Ballinger and Congdon (1981) who reported the Arizona series, found clutches averaging 5.9 eggs in those females less than 52 mm SVL (presumably in their first year), whereas the females exceeding this length averaged 10.0 eggs. The 12 Michoacan females averaged 58.3 mm (51 to 64). The species conforms with widespread trends in increasing its clutch size in the more rigorous and/or seasonal climates that occur northward or at higher altitudes.

Sceloporus undulatus. This common lizard occurs over a wide range of climates and habitats, and has become adapted to local conditions in various ways, including clutch size (Fig. 6). The main trend is from maximum clutch size in the northeastern and southwestern parts of the range to smaller clutches elsewhere, but with no extensive geographic gradients in evidence. The smallest clutches are in the subspecies *garmani* of the northern Great Plains in Nebraska, and *hyacinthinus* of the southeastern Texas woodlands, areas that are north-central and south-central respective to the overall range.

In general the species exemplifies a reproductive strategy of early maturity and high productivity, with egg clutches at frequent intervals, but the commitment to this strategy is stronger in some geographic pop-

TABLE 2. Increased clutch size from lowland to adjacent montane populations in *Sceloporus occidentalis*

Area	Latitude degrees N	Lowland Sample	Elevation	Montane Sample	Source
Jackson and Klamath counties, Oregon	42	8.20 ±0.55 (4-11) in 16	915-1220m	8.75 ±1.89 (6-12) in 24	HSF
Mendocino and Nevada counties, California	39	10.35 (5-14) in 153	2200m	13.4 ±0.57 in 24	Jameson and Allison, 1976 Schall, 1983
Great Basin; Nye County, Nevada	37	9.85 ±0.60 in 20*	2280m	11.2 in 15	Tanner and Hopkin, 1972
Contra Costa and Monterey counties, California	36 to 38	8.15 ±0.34 (6-12) in 27	880-1070m	10.3 in ?	Ruth, 1977 Davis, 1967
Kern County, California	35	6.50 ±0.53 (5-10) in 8	1528m	8.50 ±0.32 (5-10) in 16	HSF
Los Angeles County, California	34	7.23 in 43	1600m	8.70 in 41	Goldberg, 1974
San Diego County, California	33	7.00 ±0.50 (4-10) in 8	1830m	7.50 ±0.62 (4-11) in 10	HSF

* No localized lowland sample available; the 20 specimens were from scattered localities in SE Idaho, E Oregon and Nevada.

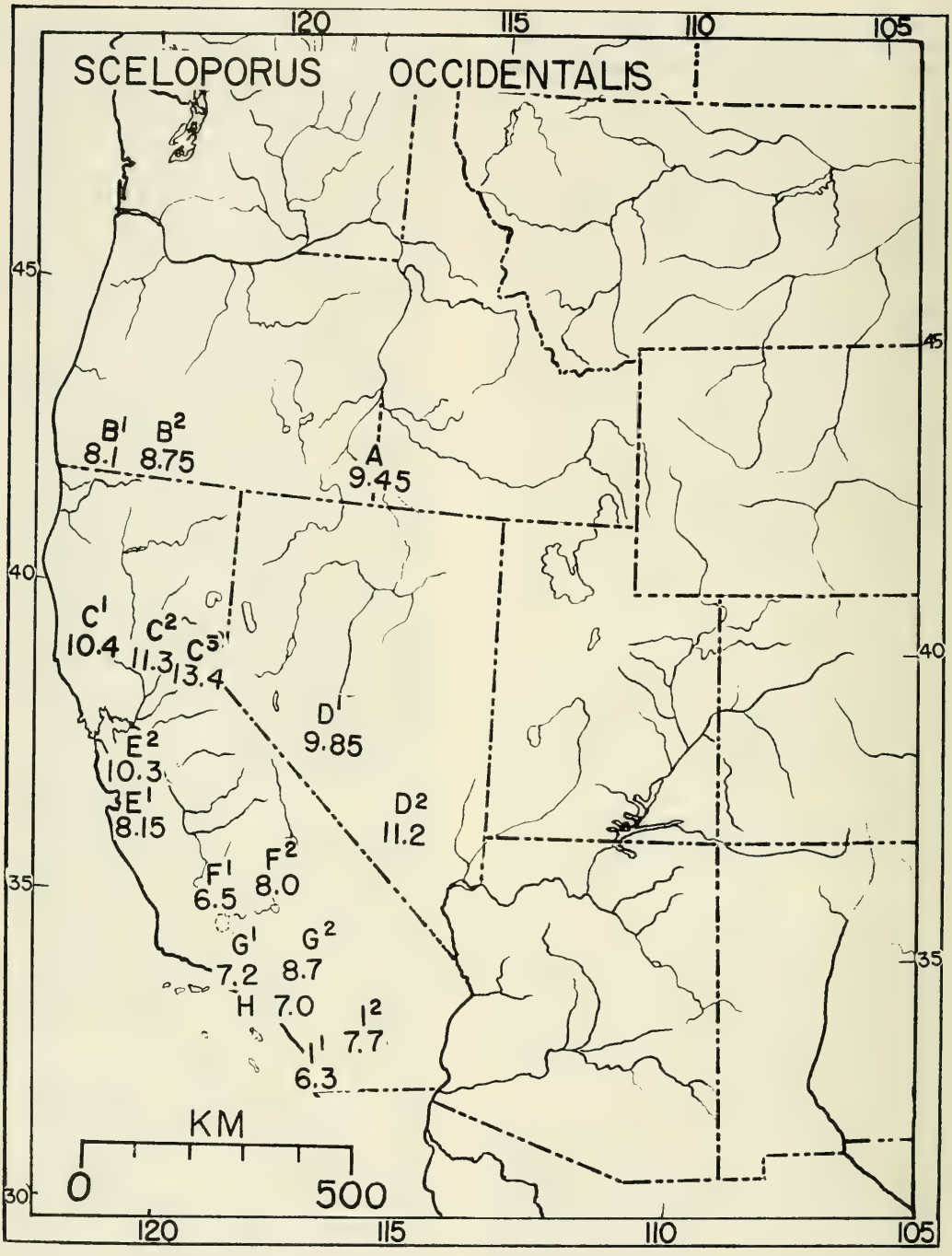

FIG. 5.—Map showing geographic variation in clutch size in *Sceloporus occidentalis*. A. Idaho, E Oregon, NW Nevada *(longipes)* **9.45** in 16; B^1. SW Oregon lowland *(occidentalis)* **8.1** ±0.6 (4-14) in 17; B^2. SW Oregon montane *(occidentalis)* **8.75** ±1.9 (5-12) in 24; C^1. N California, Mendocino County, coastal *(occidentalis)* **10.4** (6-14) in 153; C^2. N California, Donner Pass, montane *(occidentalis)* **11.3** ±0.4 in 41; C^3. N California, Donner Pass, higher montane *(occidentalis)* **13.4** ±0.6 in 24; D^1. Nevada and neighboring areas, valleys and low mountains *(longipes)* **9.85** ±0.6 in 7; D^2. S Nevada, Ranier Mesa, high montane *(longipes)* **11.2** (7-15) in 15; E^1. central California coast, Monterey County *(bocourti)* **8.15** ±0.34 (6-12) in 27; E^2. central California montane, Mount Diablo *(longipes)* **10.30;**

ulations than in others. Table 3 shows several such parameters. *S. undulatus* differs from most iguanids in having females larger than males, but the size ratio of the sexes varies geographically. Having relatively large females as one aspect of a reproductive strategy to increase egg production is a trait of the subspecies *elongatus* and *undulatus*. Reproductive effort is greatest in *garmani* and *hyacinthinus*. Time to maturity is shortest and clutches per season maximum in southern *hyacinthinus* and *garmani*.

Evidence concerning the effect of altitude on clutch size in *S. undulatus* is somewhat contradictory. The Great Plains subspecies *garmani* has a smaller clutch ($\bar{x} = 5.5 \pm 0.2$ in 63 from western Nebraska) than *erythrocheilus* of the adjacent Rocky Mountains in central Colorado ($\bar{x} = 9.7$ in 53). However, Colorado *erythrocheilus* from higher altitudes, above 1,400 m, were found to have a slightly lower mean ($\bar{x} = 9.4$ in 36) than those from below 1,400 m ($\bar{x} = 10.2 \pm 0.4$ in 17). In southwestern New Mexico the plains-living subspecies *consobrinus* produces a larger clutch ($\bar{x} = 9.9$ in 39) than the adjacent montane *tristichus* ($\bar{x} = 7.2$ in 29; Vinegar, 1975).

The Florida scrub lizard, *Sceloporus woodi*, is a southeastern representative of *S. undulatus* and hybridizes with it sparingly where their ranges and habitats overlap on the Ocala National Forest. The relatively small clutch of *S. woodi*, $\bar{x} = 4.25$ (2-8) in 162, is thought to be correlated with its small body size and terrestrial habits (Jackson and Telford, 1974). Three clutches per season is believed to be usual. Females mature in their first year. Clutch weight averages 19% of body weight, contrasted with 23% to 27% in *S. undulatus* populations. Terrestrial lizards adapted to a cursorial life style can less well afford a heavy burden of eggs than can those that are cryptic and sluggish or those that are scansorial. Relative clutch mass is less in cursorial types, with the result that young are either fewer or smaller, or both.

Sceloporus virgatus is still another member of the *S. undulatus* group, a small, monotypic species replacing *undulatus* in southeastern Arizona and adjacent Mexico. The habitat is in rocky terrain along intermittent streams in mountainous areas. It normally produces only one clutch per year, and oviposition is timed to the arrival of the rainy season. Mean clutch is 9.5 ± 0.2 (4-16) in 184. Reproduction in yearling females is variable and depends upon their growing to mature size early enough in the season; 51% were fecund in 1970 and 1972, 14% in 1971 and 56% in 1973. Relative

TABLE 3. Parameters of reproductive strategy in geographic populations of *Sceloporus undulatus*

Subspecies	Habitat & "Life Style"	FMR*	Reproductive Effort	Time to Maturity in ♀	Clutches per Season
undulatus *hyacinthinus*	scansorial in open woodland	110	.25	first year	1 or 2 (N), up to 5 (S)
garmani	sandhills, plains	107	.27	first year	2 or more
consobrinus	arid grassy plains	101	.21	second year	4 (?)
elongatus	scansorial	112	.23	second year	_____
erythrocheilus	on			second year	_____
tristichus	rocks	107	.22	second year	2 (?)

* Female-to-male ratio, length SVL percentage.

FIG. 5 (continued). F[1]. California, Kern County, lowland *(biseriatus)* **6.5** ±0.6 (5-10) in 15; F[2]. California, Kern County, montane *(biseriatus)* **8.0** ±0.3 in 13; G[1]. California, Los Angeles County lowland *(longipes)* **7.2** in 43; G[2]. California, Los Angeles County, montane *(longipes)* **8.7** in 41; H. S California, San Bernardino Mountains *(longipes)* **7.0** ±0.6 (3-11) in 14; I[1]. California, San Diego County, lowland *(longipes)* **6.3** ±0.8 (6-9) in 6; I[2]. California, San Diego County, montane *(longipes)* **7.7** ±0.6 (4-13) in 17.

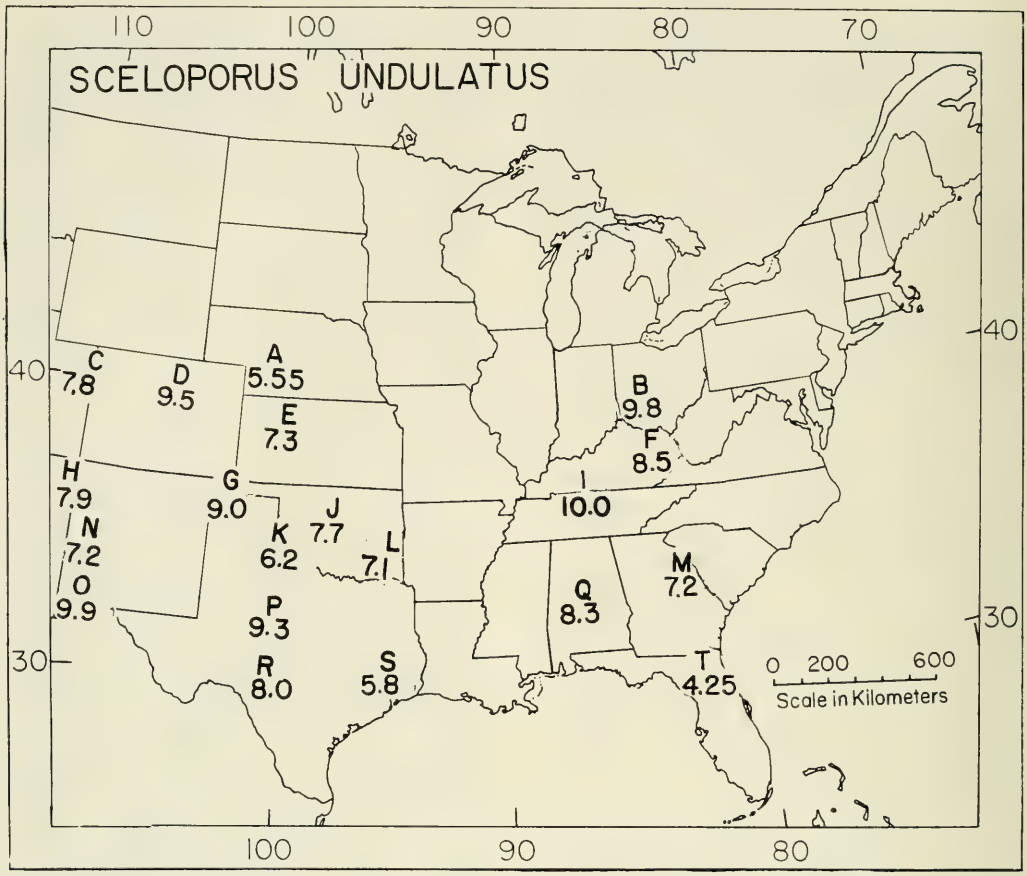

FIG. 6.—Map showing geographic variation in clutch size in *Sceloporus undulatus* and *S. woodi*. A. Nebraska *(garmani)* **5.55** ±0.2 in 63; B. Ohio, Indiana, Illinois *(hyacinthinus)* **9.8** ±0.7 (6-11) in 11; C. E Utah and W Colorado *(elongatus)* **7.8** in 10; D. central Colorado *(erythrocheilus)* **9.5** (4-15) in 53; E. Kansas *(garmani)* **7.3** (3-?) in 32; F. Kentucky *(hyacinthinus)* **8.5** in 19; G. W Oklahoma *(erythrocheilus)* **9.0** ±1.1 (4-13) in 7; H. N New Mexico and Arizona *(consobrinus)* **7.9** in 14; I. central Tennessee *(hyacinthinus)* **10.0,** sample size unknown; J. central Oklahoma *(garmani)* **7.7** ±0.6 (5-12) in 11; K. SW Oklahoma *(consobrinus)* **6.2** ±0.5 (3-8) in 13; L. SE Oklahoma *(hyacinthinus)* **7.1** ±0.7 (4-12) in 13; M. Georgia and South Carolina *(undulatus)* **7.2** (6-11) in 24; N. SW New Mexico, montane *(tristichus)* **7.2** ±0.3 in 29; O. SW New Mexico valley *(consobrinus)* **9.9** ±0.4 in 39; P. central Texas *(consobrinus)* **9.3** in 18; Q. central Alabama *(undulatus)* **8.3** in 61; R. S-central Texas *(consobrinus)* **8.0,** sample size unknown; S. SE Texas *(hyacinthinus)* **5.8,** sample size unknown, T. N Florida *(woodi)* **4.25** (2-8) in 162.

clutch mass was 29% in a sample of 89 females (Vinegar, 1975b).

Sceloporus variabilis. The three samples available to show clutch size in this small iguanid represent the northern and southern ends of the range, and an intermediate area.

Northern (Texas, Uvalde County, 29°N) $\bar{x} = 4.7$ in ?

Central (Mexico, Veracruz, 20°N) $\bar{x} = 3.2 \pm 0.3$ (2-5) in 10

Southern (NW Costa Rica, Guanacaste, 10°N) $\bar{x} = 3.2 \pm 0.5$ (1-5) in 8

In Texas a female normally produces two clutches per season and egg-laying is concentrated in late March and in June. In the tropical climate of Costa Rica egg-laying is continuous during the wetter part of the year (varying locally) but ceases during the dry season, January through April. Some of the tropical and subtropical populations occur at high altitudes, but no information is available concerning the effect of altitude on clutch size or the timing of egg-laying.

Two near relatives in the *Sceloporus variabilis* group are *S. chrysostictus* and *S. cozumelae* of the Yucatan region in south-

eastern Mexico; their mean clutch sizes are 2.4 ±0.5 (1-4), N = 16; and 1.8, N = 12, respectively. The remarkably small clutch of *cozumelae* is presumably correlated with its insular range on Isla de Cozumel, Quintana Roo, in the Caribbean.

Scincella lateralis. Several samples to show clutch size in different areas are available for this small forest skink. The main trend seems to be an increase in number of eggs to the north. Sexual maturity is attained in the first year. Potentially there are two clutches per season in the northern part of the range and at least four clutches in the south. Number of eggs per clutch varies from 1 to 7, with the highest numbers in those produced early in the season, and in those of large (and probably old) females. The following clutch sizes were found in samples from different parts of the range.

North-central (eastern Kentucky)
$\bar{x} = 3.9$ in 10
Northwestern (Kansas and Missouri)
$\bar{x} = 3.8 \pm 0.2$ (1-6) in 31
West-central (Arkansas and Oklahoma)
$\bar{x} = 2.4 \pm 0.2$ (1-6) in 17
Southwestern (Texas) $\bar{x} = 3.0$ in 68
South-central (southern Louisiana)
$\bar{x} = 3.2$ in 41
Southeastern (northern Florida)
$\bar{x} = 2.6$ (sample size not recorded)

In the series examined, the northernmost, those from Kansas, had the greatest body size ($\bar{x} = 48.9 \pm 0.8$ mm in 37) and the females that were relatively largest compared with male counterparts (female-to-male ratio 113.5%), both traits part of a strategy for increased reproductive output, compensating to some degree for the shortened season of activity.

Sphenomorphus cherriei. The small clutch of this neotropical skink may be subject to some geographical change.

Northern (Guatemala)
$\bar{x} = 2.8 \pm 0.2$ (2-3) in 4
Southern (Costa Rica)
$\bar{x} = 2.2 \pm 0.1$ (1-3) in 29

Many of the Costa Rica records were from Turrialba where the breeding season extended over much of the year but excluded the drier part, December through March. On the Caribbean coast of Costa Rica, in a wetter climate, reproduction seemingly continued through the entire year. In Guatemala, with a more sharply seasonal climate, it would seem that the breeding season is shorter and clutches are correspondingly larger.

Tropidurus albemarlensis and **T. delanonis.** The seven species of Galapagos lava lizards are probably all derived from a common ancestor that reached the archipelago from the South American mainland since there is no evidence of former land connection. Information concerning clutch size is available for only two of the species.

Santa Cruz Island *(albemarlensis)*
"usually two eggs per clutch but occasionally three or four"
Indefatigable Island *(albemarlensis)*
$\bar{x} = 2.0$ (2 in each of 5)
Hood Island *(delanonis)* $\bar{x} = 4.36$ (3-6) in 36

T. albemarlensis occurs on several of the larger and more centrally located islands, but each of the other six species is endemic to a single island. While *T. albemarlensis* is relatively small (average male SVL 82 mm, female 65 mm), *T. delanonis* is the largest (male 119, female 90) with the greatest sexual dimorphism in size. Eggs of *T. delanonis* average 26.3 mm long vs 19.8 mm for those of *albemarlensis*, hence they are roughly proportional to sizes of the females despite the larger clutch of *T. delanonis*. The latter species thus contributes the greater reproductive effort. Although predation pressure is often relatively light in insular habitats, predators including a hawk *(Buteo galapagoensis)*, a snake *(Dromicus biserialis)*, a mockingbird *(Nesomimus macdonaldi)* and a centipede *(Scolopendra galapagoensis)* are important in the ecology of *T. delanonis* (Werner, 1977). Presumably predation is at least equally important on the larger islands where *T. albemarlensis* occurs, although data are not available to verify this supposition.

Uma notata, U. inornata and **U. scoparia.** These three closely related species of sand lizards are allopatric and are confined to desert sand dunes of southern California and adjacent areas. Their reproduction is known through the studies of Mayhew (1965, 1966a, 1966b).

Northern (Dry Lake, San Bernardino County, 426 m, *scoparia*)
$\bar{x} = 2.6$ in 90

Central (Coachella Valley, Riverside County, *inornata*)
$\bar{x} = 2.4 \pm 0.1$ (2-4) in 22
Southern (Algodones Dunes, Imperial County, 90 m, *notata*) $\bar{x} = 2.1$ in 90

In these three samples, female lengths SVL averaged, respectively, 83, 81, and 76 mm in series of 200 or more. Hence clutch size correlated closely with body size. In each population Mayhew (op. cit.) found that a few precocious females matured at an age of about one year, but in most reproduction was postponed until the second summer after hatching. Normally two or more clutches are produced in the course of a season. However, after a winter of scanty precipitation, resulting in unusually sparse annual vegetation, and scarcity of insect food, reproduction is curtailed.

Urosaurus graciosus. Several series of clutches of this small scansorial desert iguanid indicate extensive geographic variation, but trends need to be clarified with further material.

Central (southern Arizona)
$\bar{x} = 4.15$ (2-8) in 43
Western (lower Colorado River)
$\bar{x} = 5.3$ (3-10) in 23

The latitudinal scope of the records is small, and is not well suited to show north-south change. The records seem to show reduction of clutch from west to east.

Urosaurus ornatus. Seven sizable samples, some of them composites, are shown for this small arboreal iguanid, widespread in the southwestern United States (Fig. 7). Clutch size averages from 3.9 eggs in Mesa Verde National Park, southwestern Colorado, and south-central Arizona to more than 9 in southwestern New Mexico, but there seems to be no latitudinal trend. Perhaps productivity is controlled mainly by the amount of precipitation locally, as mean clutch size has been found markedly lower in drought years than in unusually wet years in the same locality (Martin, 1973, 1977). Southern populations are reproductive from March through mid-August, and probably three or four successive clutches are normal. Early clutches are largest, and later clutches decline to two-thirds or less (Martin, 1973).

Uta stansburiana. For this species a dozen geographical samples, many of them composites, are available, well distributed throughout the range, with large series of clutches available for most of them. For 2,269 clutches, the mean is 3.5 eggs per clutch, varying from 2.8 to 4.3 in different samples, but with no clear-cut trends (Fig. 8). Oregon, Washington, Nevada, southern New Mexico, and most of California have relatively low means, whereas northwestern Utah, southwestern Arizona, western Texas, and Riverside County, California, have relatively large clutches, and the largest of all were from the small sample from high altitude on Ranier Mesa, southern Nevada.

Body size varies somewhat throughout the range (Parker and Pianka, 1975) but with no definite latitudinal trend. Where body size is larger than usual, as in southern Arizona and northwestern Utah, clutch size also is relatively large. Relative size of the sexes also is subject to geographic variation. Females average a little larger than males in northwestern Utah, but elsewhere average somewhat smaller than males, with the minimum ratio of about 87 per cent SVL occurring in the southwestern part of the range. Studies by Tinkle (1967), Parker and Pianka (1975), and Nussbaum and Diller (1976) have indicated that those populations occurring in relatively cool climates with short growing seasons, as in north-central Oregon, and in the vicinity of Grantville, Utah, have territoriality and male aggression relatively weakly developed compared with those living farther south where the growing season is longer. Hence selective pressure for relatively large male size is relatively weak in the north, and the female may produce only one clutch annually, whereas three clutches are normal in warm southern areas.

Montane populations may tend to have increased clutch size, compared with nearby lowland counterparts. For instance in desert valleys of southern Nevada, 521 clutches averaged 3.25 eggs, but on Ranier Mesa, 2286 m, in that area, five clutches averaged 4.85 eggs. Unfortunately the montane sample is too small to be reliable in this instance. A sample from the San Gabriel Mountains, southern California, averaged 3.50 ($N = 162$), about the same as for nearby lowland samples for coastal southern California.

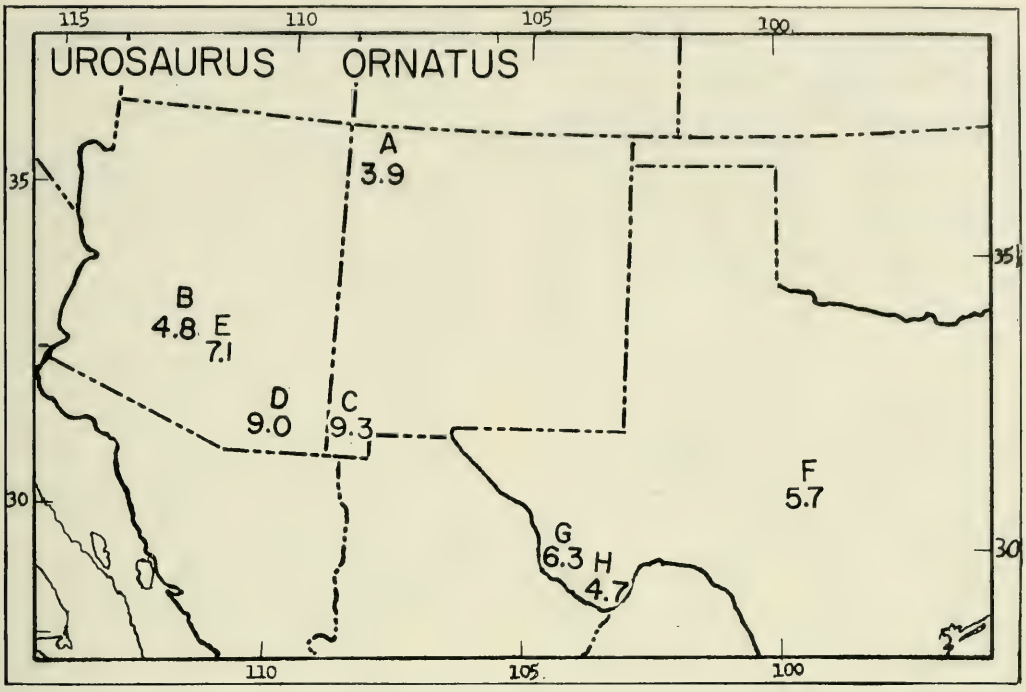

FIG. 7.—Map showing geographic variation in clutch size in *Urosaurus ornatus*. A. NW New Mexico *(wrighti)* **3.9** (2-6) in 9; B. Arizona, Phoenix and vicinity *(symmetrica)* **4.8** (2-7) in 24; C. southern New Mexico, Hidalgo County *(linearis)* **9.3** ±0.2 in 264; D. southeastern Arizona, Chiricahua Range *("chiricahuae")* **9.0** ±0.2 in 104; E. Arizona, Maricopa County *(linearis)* Sunflower **7.1** ±0.3 in 101; F. central Texas, Edwards Plateau *(ornatus)* **5.7** in 369; G. western Texas, Presidio County *(schmidti)* **6.3** ±0.2 (5-10) in 22; H. Texas, Big Bend National Park *(schmidti)* **4.7** ±0.1 in 189.

In a population near Anapra, Dona Ana County, south-central New Mexico, Worthington (1982) made comparisons of the body sizes of adults and clutch sizes in the dry year of 1971 vs the wet years of 1973 and 1975. Both males and females averaged approximately 12% larger (SVL) in the wet years, when insect food was more abundant. Clutches averaged 2.5 ±0.4 (2-3, N = 8) in 1971, and averaged 3.8 ±0.3 (3-5, N = 20) in 1973.

Xantusia riversiana. The island night lizard occurs only on the three Channel Islands, Santa Barbara, San Clemente and San Nicolas off the coast of southern California. It is in a different subgenus, sometimes considered a separate genus, from the mainland species of *Xantusia*. Bezy et al. (1980) have shown differences in clutch size among the three populations, with corresponding size differences (shown below in millimeters SVL in adult females).

Santa Barbara	$\bar{x}$ = 3.3 (3-4) in 4 (83.4 ±1.3 in 31)
San Clemente	$\bar{x}$ = 4.0 ±0.2 (2-6) in 30 (84.2 ±0.4 in 294)
San Nicolas	$\bar{x}$ = 5.5 ±0.6 (3-9) in 13 (88.9 ±0.8 in 86)

Santa Barbara Island, having the smallest clutches, is by far the smallest of the three islands. San Nicolas is the most remote from the mainland; San Clemente is almost as far and is about twice the size of San Nicolas.

SNAKES

The reproductive strategies of snakes are influenced by the fact that all are predators and ingest their prey entire; that the sexes are usually disparate in size, with females moderately to greatly exceeding males (but with males the larger in occasional colubrine, elapine and crotaline genera); that the sprawling posture alleviates the burden of gravity; that these animals have the capacity to store abdominal fat and to fast for

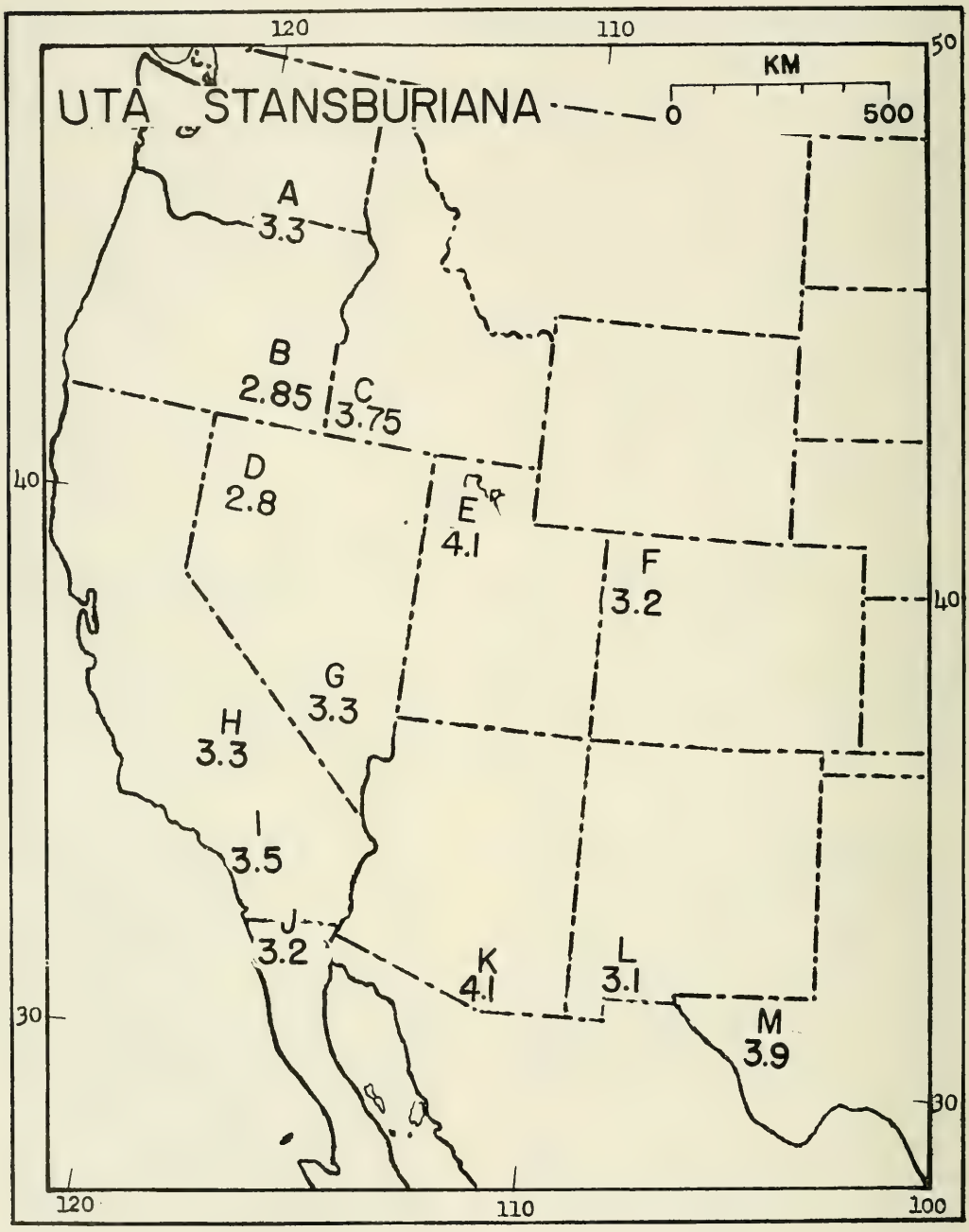

FIG. 8.—Map showing geographic variation in clutch size in *Uta stansburiana*. A. N Oregon and E Washington and Idaho *(nevadensis)* **3.3** in 97; B. SE Oregon *(nevadensis)* **2.85** in 27; C. SW Idaho *(nevadensis)* **3.75** in 194; D. NW Nevada *(nevadensis)* **2.8** in 26; E. NW Utah *(stansburiana)* **4.1** in 184; F. NW Colorado *(uniformis)* **3.2** in 256; G. S Nevada *(elegans)* **3.3** in 533; H. California, Kern County **3.3** in 25; I. S California, San Gabriel Mountains *(elegans)* **3.5** in 162; J. S California and Baja California *(elegans)* **3.2** in 118; K. S Arizona *(elegans)* **4.1** in 121; L. S New Mexico *(stejnegeri)* **3.1** in 97; M. W Texas *(stejnegeri)* **3.9** in 428.

extended periods. Viviparous reproduction is fairly common, occurring in diverse groups, but oviparity is characteristic of the majority. Relative clutch mass averaged .31 (.11 to .44 in 106 populations checked by Seigel and Fitch, 1984). Relative clutch mass (clutch weight divided by total weight of female parent) was found to average markedly higher (.35) in 52 oviparous populations than in 54 that were live-bearers (.28). On the other hand broods were found to average more young in the live-bearers than in the egg-layers. It seems to be a general rule, both within species and in higher categories that relatively large snakes produce relatively large numbers of eggs or young. However, in the majority of instances, neither the sizes of the females involved in the samples nor the mean sizes characteristic of their local populations were known. A little known aspect of snake reproduction that is probably closely correlated with clutch size is the frequency of reproduction in individual females. For Temperate Zone species an annual cycle is generally assumed, but there is evidence (mainly from captive individuals) of occasional second clutches, while evidence from both natural populations and captives indicates that females of populations that are basically on an annual cycle may occasionally or frequently miss a year.

Agkistrodon contortrix. Several samples are available from various parts of the range, demonstrating a consistent geographic trend in the litter size of this species.

Northeastern (Connecticut, Massachusetts, New Jersey, Pennsylvania, Maryland, Virginia; *mokeson*) $\bar{x} = 6.4 \pm 0.3$ (2-14) in 41
Upper midland (Ohio, Illinois, Kentucky; *mokeson*) $\bar{x} = 6.6 \pm 0.9$ (3-11) in 10
Southeastern (North Carolina, Georgia, Mississippi, Louisiana; *contortrix*) $\bar{x} = 6.6 \pm 0.5$ (5-11) in 17
Northwestern (Missouri; *phaeogaster*) $\bar{x} = 5.6$ (3-11) in 20
Northwestern (northeastern Kansas; *phaeogaster*) $\bar{x} = 5.2 \pm 0.2$ (2-13) in 88
West-central (Oklahoma and Texas; *laticinctus*) $\bar{x} = 3.8 \pm 0.5$ (1-7) in 17
Southwestern (western Texas; *pictigaster*) $\bar{x} = 3.1 \pm 0.3$ (2-4) in 8

Seemingly litter size increases from a minimum in the southwestern part of the range to maxima eastward and northeastward (Fig. 9). Body size is relatively small in the three western subspecies, and especially in *A. c. laticinctus* and *A. c. pictigaster,* and no doubt litter size is closely correlated with body size.

A. c. phaeogaster of northeastern Kansas is the best known ecologically. In this population most females mature and breed in their third year, but some do not mature until their fourth year. A biennial breeding cycle is the most common pattern, but with frequent deviations. The records of marked individuals recaptured in subsequent years showed that individuals may produce litters in two successive years, or may go for two years without producing young (Fitch, 1970). Because the growing season is much longer in the southern part of the range than in the northern part, southern populations might be expected to mature earlier and to produce litters more frequently, on the average. However, such geographic differences have not yet been demonstrated.

Agkistrodon piscivorus. Both local series and isolated records are available to show litter size in the cottonmouth.

Northeastern (southeastern Virginia; sbsp. *piscivorus*) $\bar{x} = 7.7 \pm 0.4$ in 24
Western and northwestern (Illinois, Kentucky, Missouri, Oklahoma, Louisiana, Texas; sbsp. *leucostoma*) $\bar{x} = 6.8 \pm 0.8$ (2-15) in 21
Southeastern (Florida; sbsp. *conanti*) $\bar{x} = 6.6 \pm 0.3$ (3-12) in 31
Southeastern insular (Florida, Cedar Keys; sbsp. *conanti*) $\bar{x} = 5.6 \pm 0.3$ (3-8) in 24

The Florida records are those of Allen and Swindell (1948) and Wharton (1966) whereas the *A. p. leucostoma* records are from a variety of sources. The ten most northern *leucostoma* records have a mean of 6.8, slightly higher than for those of the Gulf Coast.

The Cedar Key islands population reported upon by Wharton (1966) is probably atypical of mainland populations in several respects. These islands lie 11 km offshore in the Gulf of Mexico, and have a meager fauna of resident vertebrates. Cottonmouths subsist largely on marine fishes and their discarded remains, fallen to the ground beneath the large rookeries of cormorants,

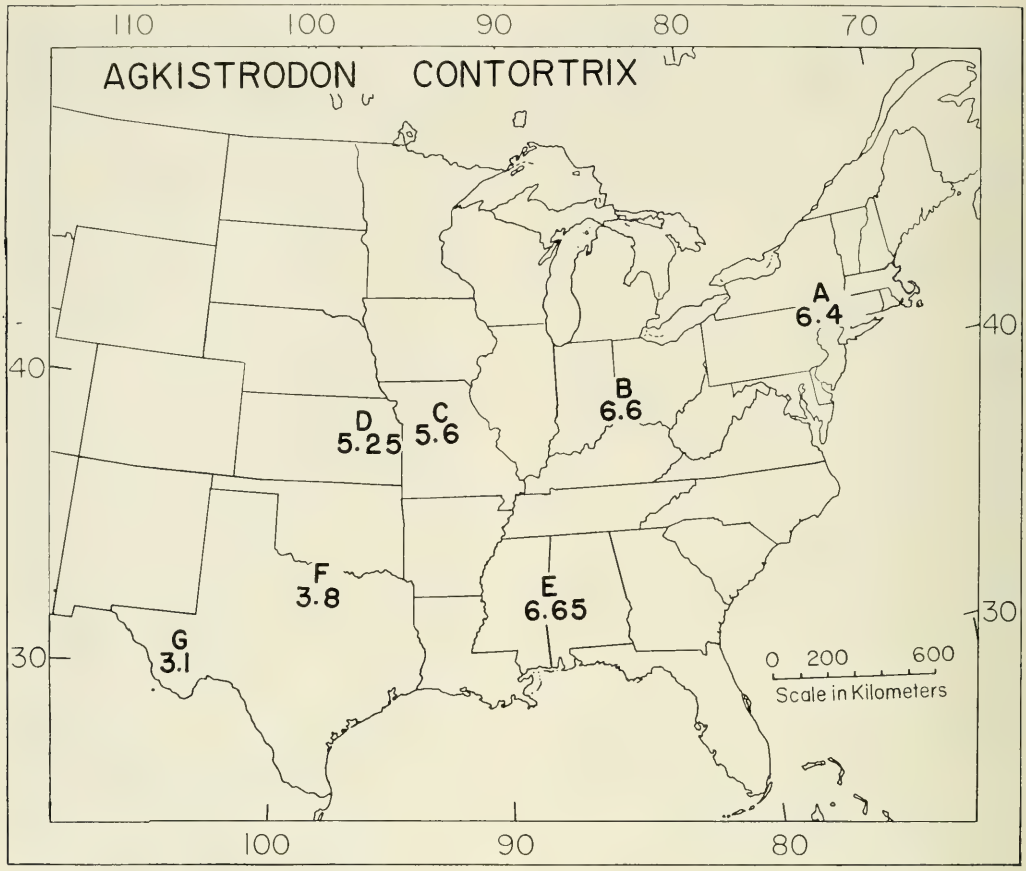

FIG. 9.—Map showing geographic variation in litter size in *Agkistrodon contortrix*. A. northeastern states (Conn., Mass., Md., N.J., Pa., Va.) *(mokeson)* **6.4** ±0.35 (2-14) in 41; B. Ill., Ky., Ohio *(mokeson)* **6.6** ±0.9 (3-11) in 10; C. Missouri *(phaeogaster)* **5.6** (3-11) in 20; D. NE Kansas *(phaeogaster)* **5.25** ±0.2 (2-13) in 88; E. southeastern states (Ga., La., Miss., N.C.) *(contortrix)* **6.65** (5-11) in 17; F. Okla., Texas *(laticinctus)* **3.8** ±0.5 (1-7) in 17; G. W Texas *(pictigaster)* **3.1** (2-4) in 8.

herons, and egrets. Nesting of these water birds occurs from mid-February through August. In seeming adaptation to their island environment the Cedar Key cottonmouths average slightly larger than their mainland counterparts, and their neonates average markedly larger, mean total length 332 mm (324-350), N = 19, vs 203-279.

Blem (1981) studied the cottonmouth's reproduction at the northeastern extreme of its range in southeastern Virginia. He found litters there to be relatively large, but with neonates small (mean 211.3 mm SVL, 17.3 grams, N = 80). He speculated that reduced size of neonates could be interpreted as an evolutionary compromise for maintaining litter size while reducing the expenditure of energy per litter. He found evidence of heavy mortality during the winter in first-year snakes.

Arizona elegans. Records of clutches in this desert snake are few and scattered. The only local series is that of Aldridge (1979); 7 clutches from west-central New Mexico averaged 8.4 ±0.7 (3-6). These combined with other records, suggest geographic differences.

Eastern (Oklahoma, New Mexico, Texas; sbsp. *elegans, blanchardi*)
$\bar{x}$ = 9.0 (6-12) in 10

Western (California, Arizona; sbsp. *candida, eburnata, occidentalis*)
$\bar{x}$ = 7.8 ±1.8 (3-23) in 10

Possibly clutches average larger in the east-

ern populations, but by far the largest clutch recorded was that of a California snake.

Boa constrictor. This large tropical snake occurs in a great variety of habitats and climates and is subject to various sorts of geographic variation. As in other large and prolific boids, litter size is much influenced by the size and age of the female. Newly matured individuals produce relatively small litters compared with large old adults, and this probably obscures geographic variation in the small samples available.

Mexico and Central America
$\bar{x} = 17.8 \pm 3.4$ (10-36) in 6
South America (Trinidad, Peru)
$\bar{x} = 30.3 \pm 7.3$ (6-63) in 6

Whether northern populations of this boa actually have litters averaging much smaller than those of South American rain forests, and whether body size is smaller in the north must remain undetermined until larger samples are available.

Bothrops atrox and **B. asper.** Regardless of taxonomic status the northern and southern fer-de-lances probably differ in size of litter.

Costa Rica *(asper)* 48-86
Honduras, Panama *(asper)*
$\bar{x} = 58$ (32-71) in 4
Trinidad, Guyana, Venezuela, Peru *(atrox)*
$\bar{x} = 26.2$ (8-57) in 19

These figures suggest that the Central American snakes may have at least twice as many young per litter as their near relatives from South America, but more data are needed.

Carphophis amoenus and **C. vermis.** The conspecificity of these worm snakes is still controversial. Samples of clutch size are available as follows:

Eastern (New Jersey, Connecticut, Maryland, Alabama; sbsp. *amoenus*)
$\bar{x} = 4.1$ (2-8) in 9
Central Kentucky; sbsp. *helenae*)
$\bar{x} = 2.8$ (1-4) in 21
Western (Northeastern Kansas; sp. *vermis*)
$\bar{x} = 2.9$ (1-5) in 118

Increase in clutch size from inland populations to those of the East Coast is indicated. The Kansas records are from Clark (1970). Reduction of clutch size during development was shown by his data. The following are from Clark's figures, with the addition of 30 museum specimens.

Ovarian follicles and early oviducal eggs dissected $\bar{x} = 3.3$ in 47
Mature oviducal eggs dissected
$\bar{x} = 3.0 \pm 0.09$ (1-5) in 84
Eggs laid $\bar{x} = 2.6 \pm 0.15$ (1-4) in 34

Coluber constrictor. One large sample of clutches and several smaller samples are available for this widely distributed snake.

Northeastern (New York, Ohio, Maryland, Kentucky, North Carolina; sbsp. *constrictor*) $\bar{x} = 17.2 \pm 1.9$ (7-31) in 13
North-central (Illinois, Missouri; sbsp. *flaviventris*) $\bar{x} = 11.5$ (7-22) in 13
Southeastern (South Carolina, Florida, Georgia; sbsp. *priapus*)
$\bar{x} = 12.0 \pm 1.5$ (5-22) in 12
Western (Kansas; sbsp. *flaviventris*)
$\bar{x} = 11.40$ (5-22) in 68
Southwestern (Louisiana, Oklahoma, Texas; sbsp. *flaviventris* and *anthicus*)
$\bar{x} = 13.3 \pm 1.7$ (6-27) in 12

Maximum clutch size seems to be in the northeastern states, with reduction to the south and especially to the west. Body size is relatively large in the northeastern racers that lay relatively large clutches.

Coluber mormon. The western racer has much smaller clutches than the eastern species, and may have some geographic variation within its extensive range.

Northwest Coast (British Columbia, Oregon, northern California)
$\bar{x} = 5.4 \pm 0.4$ (2-10) in 27
Great Basin (northern Utah)
$\bar{x} = 6.4 \pm 0.3$ (4-11) in 43
Southwest Coast (central and southern California) $\bar{x} = 6.1 \pm 0.9$ (4-13) in 11

These figures suggest possible trends toward increased clutch sizes inland and southward.

Coniophanes fissidens. These small, diurnal, forest-floor colubrids occur from tropical Mexico to Peru, and reproductive data have been assembled by Zug, Hedges and Sunkel (1979). Their data are here partitioned for comparison of northern and southern samples.

Northern (Veracruz and Chiapas, Mexico; Guatemala) $\bar{x} = 2.5 \pm 0.2$ (1-5) in 34
Southern (Costa Rica, Panama, Ecuador)
$\bar{x} = 3.2 \pm 0.6$ (1-7) in 10

A northward decrease is indicated. Local samples were too small for the authors to judge whether reproduction was seasonal. The climatic difference implied in the "northern" and "southern" groups, with more seasonal climates in the north is deceptive and is at least partially offset by the fact that some snakes came from higher alti-

tudes. Rearrangement of the records according to altitude led to the following comparison.

Montane (1000-2000 m), Guatemala, Panama $\bar{x} = 3.1 \pm 0.5$ (1-5) in 8

Lowland tropical and subtropical (below 1000 m), Mexico, Guatemala, Costa Rica, Panama, Ecuador $\bar{x} = 2.5 \pm 0.2$ (1-7) in 36

As in various other reptiles, the clutch seems to increase at higher altitudes. Zug et al. (1979) presented a table showing gravid females or hatchlings in January, March, May, June, July, August, September, and November at lower altitudes (indicative of possible year round breeding) but for the smaller sample of high altitude specimens there are comparable records only for January, March, April, and May.

Crotalus atrox. One local sample of litters and two composite samples are available.

Northwestern Texas, Garza, Lynn, Nolan and Scurry counties $\bar{x} = 13.2$ in 62

Central and southern Texas, New Mexico, Arizona $\bar{x} = 9.00 \pm 0.66$ (4-21) in 33

Northern Mexico $\bar{x} = 14.3$ (6-25) in 9

The records suggest southward increase in litter size and decrease westward.

Crotalus cerastes. The available records show no geographic variation in litter size in the sidewinder.

Northern (Mohave Desert, *cerastes*) $\bar{x} = 10.8 \pm 0.1$ (7-18) in 10

Southern (Colorado Desert and Arizona, *laterorepens* and *cercobombus*) $\bar{x} = 9.0 \pm 0.5$ (5-16) in 28

All records are from Klauber (1956).

Crotalus durissus. The widely distributed neotropical rattlesnake has two closely related geographic representatives that are currently considered to be distinct species. *C. unicolor* is a relatively small and pale colored rattlesnake of Aruba Island, Netherlands West Indies, and *C. vegrandis* is a dwarfed endemic of the Venezuelan llanos.

Mexico and Central America *(durissus* and *totanacus)* $\bar{x} = 24.2 \pm 6.1$ (10-47) in 6

South America *(terrificus)* $\bar{x} = 18.2 \pm 3.1$ (10-31) in 6

Venezuela, Uracoa *(vegrandis)* $\bar{x} = 4.2 \pm 0.5$ (2-8) in 16

Aruba Island, Netherlands West Indies *(unicolor)* $\bar{x} = 6.2 \pm 0.9$ (2-14) in 15

As in many other instances, reduction in number of young per litter is associated with reduced adult size, and also with insular occurrence. It is unknown whether there is a switch from a biennial reproductive cycle in northern populations living in areas of marked seasonal change to an annual cycle in relatively aseasonal equatorial climates.

Crotalus horridus. The four local samples available provide evidence of geographic variation in litter size.

Northeastern (New York, Warren County) $\bar{x} = 9.3 \pm 0.5$ (4-14) in 20

Northwestern (Wisconsin, Buffalo County) $\bar{x} = 8.4 \pm 0.4$ (3-11) in 25

West-central (northeastern Kansas) $\bar{x} = 8.5 \pm 0.9$ (5-14) in 10

Southeastern (South Carolina) $\bar{x} = 12.6 \pm 0.5$ (10-16) in 16

Evidently female reproduction is biennial in some areas. In Kansas the smallest fecund females were those with strings of six rattles and lengths SVL of 800 to 900 mm, believed to be in their fourth year. Likewise in Wisconsin Keenlyne (1978) tentatively concluded that females reached maturity and produced litters in the fourth year, and the same probably applies to the South Carolina population, although Gibbons (1972) was of the opinion that maturity might be delayed until the sixth year. New York females that produced litters averaged 970 mm, SVL; Wisconsin females averaged 990 mm; those from Kansas 900; and those from South Carolina 1270. Of the 186 eggs ovulated by the 20 New York females, 149 produced living young, but 12 other young were stillborn and 25 ova were apparently infertile. In Shenandoah National Park, W. H. Martin, III, (pers. comm.) found a mean litter size of 8.5 (4-12) with females first bearing young at an age of six or seven years, and at intervals of three or four years thereafter. Average female size was 896 mm (SVL) in this population. Although the series from Wisconsin, Kansas and South Carolina suggest a northward decrease in litter, Klauber's (1956) sets of records (shown below) from scattered localities for northern *"horridus"* and southern *"atricaudatus"* do not conform with this trend:

Northern *("horridus")* $\bar{x} = 10.6 \pm 0.7$ (5-30) in 44

Southern *("atricaudatus")* $\bar{x} = 9.7 \pm 0.5$ (7-11) in 7

Crotalus lepidus. Available records indicate possible geographic variation in litter size in this southwestern rattlesnake.

Southeastern Arizona in Chiricahua range and adjacent northern Mexico *(klauberi)* $\bar{x} = 3.9 \pm 0.4$ (2-8) in 17

Mexico *(lepidus, maculatus, morulus)* $\bar{x} = 6.0 \pm 1.1$ (3-11) in 6

The samples are probably affected by differences in altitude more than by the latitudinal differences. The southern populations often occur in pine-oak forests, or even in cloud forests *(morulus)* at higher altitudes than *klauberi* or northern *lepidus* usually attain (Armstrong and Murphy, 1979). The relatively cool climate, with shortened days and seasons of activity, may be correlated with increased litter size, as in *C. triseriatus.*

Crotalus mitchelli. Litter size in the speckled rattlesnake is subject to geographic variation, as shown by the following.

Northern (California and western Nevada, *stephensi*) $\bar{x} = 8.7 \pm 0.7$ (6-10) in 6

Middle (southern California, Arizona, Baja California del Norte; *pyrrhus*) $\bar{x} = 5.5 \pm 0.4$ (4-8) in 10

Southern (Baja California del Sur, *mitchelli*) $\bar{x} = 3.6 \pm 0.5$ (2-5) in 5

Insular (Isla el Muerto, Gulf of California, Mexico; *muertensis*) $\bar{x} = 3.7$ (1-7) in 3

Seemingly there is marked decrease southward, and also in the dwarfed insular population of the Gulf.

Crotalus pricei. This small, montane rattlesnake occurs in isolated populations in somewhat different climates and habitats, and its litter size may be subject to geographic variation.

Northern; southeastern Arizona *(pricei)* $\bar{x} = 5.3 \pm 0.4$ (3-8) in 12

Southern; Durango, Chihuahua, Nuevo Leon, Mexico *(pricei* and *miquihuanus)* $\bar{x} = 6.3 \pm 0.6$ (4-9) in 7

Northward reduction is suggested by these figures. However, the main trend in litter size may be an increase from lower to higher altitude.

Crotalus ruber. Litter size in the red diamond rattlesnake undergoes marked latitudinal change.

Northern (southern California; Baja California del Norte; *ruber*) $\bar{x} = 8.7 \pm 0.73$ (3-20) in 28

Southern (southern Baja California del Sur; *lucasensis*) $\bar{x} = 3.3 \pm 0.6$ (1-5) in 15

Crotalus viridis. Several large series of broods for this common rattlesnake have been reported, and there is good evidence of extensive geographic variation (Fig. 10). Throughout the range litter size seems to be closely correlated with adult body size, which is subject to much variation. Doubtless many environmental factors affect adult size; the size and type of prey to which the local population of snakes is adapted is certainly important. *C. v. caliginis* of Los Coronados Islands is a dwarfed subspecies that preys chiefly on lizards, and its litter size is by far the most reduced, with a mean of only 2.6 young. Means as low as 5.5 have been found in *C. v. oreganus* of northern Idaho and *C. v. lutosus* of Tooele County, Utah, both dwarfed populations with adult females averaging only about 650 mm SVL. *C. v. nuntius* of northern Arizona (mean litter size 7.0) and neighboring populations of other subspecies are also conspicuously dwarfed. The most evident geographic trend is one of reduction from relatively large litters of *C. v. viridis* of the Great Plains to smaller litters in the populations of all other subspecies occurring farther west. Even in *C. v. viridis* of New Mexico, with females averaging only 640 mm SVL, mean litter size was found to be 9.5, higher than in any of the other subspecies but lower than in other *C. v. viridis* samples. There are striking differences between local populations. Thus Rahn (1942) found that *C. v. viridis* at Cheyenne, Wyoming, averaged several inches longer than did those of Klauber's (1956) large Platteville series collected 100 km farther south. Evidence that litter size increases with altitude is to be found in the mean litter of 7.5 for the Tintic Mountains of Utah, compared with the mean of 5.5 for nearby foothill dens of Tooele County.

The mean of 8.3 for Madera County, central California, is based on my counts of follicles, oviducal eggs and embryos from females 1938–1947 at the San Joaquin Experimental Range. Using the same set of data in an earlier publication (Fitch, 1949) I found an average of 9.9, but that figure included several complements in which vitellogenesis was in an early stage, with follicle lengths 5 to 14 mm, and some of these might not have developed. The 8.3

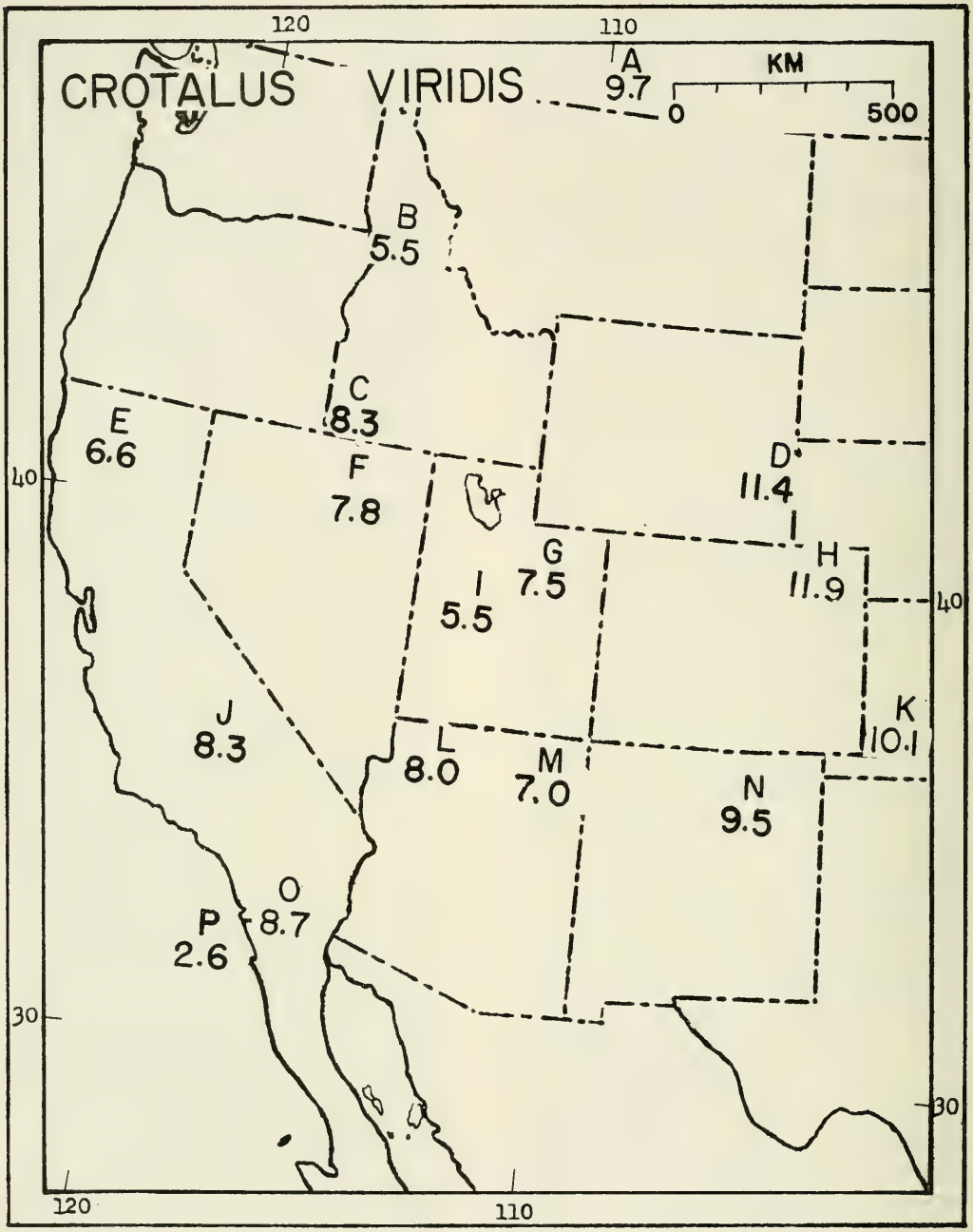

FIG. 10.—Map showing geographic variation in litter size in *Crotalus viridis*. A. Leader, west-central Sasketchewan *(viridis)* **9.7** in 53; B. N Idaho *(oreganus)* **5.5** ±0.1 in 117; C. SW Idaho *(lutosus)* **8.3**, sample size unknown; D. Great Plains (*viridis*, including sample "G" below) **11.4** (2-21) in 308; E. Northwest Coast *(oreganus)* **6.6** (1-14) in 79; F. Great Basin *(lutosus)* **7.8** (2-13) in 38; G. Utah, Tintic Mountains *(lutosus)* **7.5** (6-11) in 6; H. North-central Colorado, Platteville *(viridis)* **11.9** in 149; I. Utah, Tooele County *(lutosus)* **5.5** (2-9) in 490; J. Central California, Madera County *(oreganus)* **8.3** (2-14) in 17; K. SW Kansas *(viridis)* **10.1** ±0.8 (5-18) in 19; L. S Utah, N Arizona, NW New Mexico *(abyssus* and *cerberus)* **8.0** (6-13) in 5; M. NE Arizona *(nuntius)* **7.0** ±0.8 (3-10) in 10; N. E New Mexico *(viridis)* **9.5** ±0.6 (5-14) in 17; O. S California, Baja California del Norte *(helleri)* **8.7** (1-14) in 12; P. Baja California del Norte, South Coronados Island *(caliginis)* **2.6** ±0.4 (1-4) in 7.

mean is based upon clutches with follicles 15 to 33 mm in length.

In northern populations of *C. v. viridis* and *C. v. lutosus* a well defined biennial cycle has been demonstrated (Rahn, 1942). Females that produce young in late summer or early autumn enter hibernation with their abdominal fat bodies depleted and ovaries small, and their oviducts are enlarged, with well defined pouches where embryos have developed. During the next season of activity these parturient females do not reproduce, but gradually replenish their fat bodies, and follicles undergo vitellogenesis. By the time of the second hibernation these follicles have nearly completed their growth and are almost ready for ovulation. Evidently about half the females in a local population are fecund in any one year.

In contrast, in the southern part of the range, at least in *C. v. helleri* of San Diego County, California, *C. v. oreganus* of Madera County, and *C. v. viridis* of southwestern Kansas and eastern New Mexico, the female cycle is annual. At the time of emergence from hibernation, ovarian follicles are relatively small, often less than 10 per cent of their size at ovulation, and variable. Even where the cycle is essentially annual, a variable proportion of females do not produce in any one year, and seemingly the cycle is triggered by the accumulation of sufficient lipid reserves. Near 46°N, in northern Idaho, Diller and Wallace (1984) found that the following percentages of adult females of *C. v. oreganus* reproduced in consecutive years in three separate denning areas: 47.8%, 34.3%, 22.2%.

Diadophis punctatus. Several samples of clutches are available for this transcontinental species, but all are from the eastern half of the United States. Geographic variation is convincingly demonstrated.

Northeastern (Maine, New York, Indiana, Pennsylvania, District of Columbia; *edwardsi*) $\bar{x} = 6.5 \pm 1.0$ (1-10) in 11
Northern (northern Michigan; *edwardsi*) $\bar{x} = 3.5 \pm 0.2$ (1-7) in 202
Central (northeastern Kansas; *arnyi*) $\bar{x} = 3.9 \pm 0.1$ (1-10) in 300
Eastern (Kentucky; *edwardsi*) $\bar{x} = 3.6 \pm 0.3$ (2-6) in 15
Southeastern (Florida; *punctatus*) $\bar{x} = 5.2 \pm 0.4$ (2-10) in 23

The means shown above seem to indicate a trend from smaller clutches in inland areas to larger clutches in coastal regions. Doubtless clutch size is correlated with body size, and that in turn is closely linked with food habits and general ecology. The northeastern snakes of the subspecies *edwardsi* are relatively large. However, the Florida snakes of the subspecies *punctatus* are the smallest of the five populations sampled.

Dipsas catesbyi. This slender, arboreal snail-eater is widely distributed in the South American tropics. Zug, Hedges and Sunkel (1979) have published reproductive data from 10 localities. A geographical partitioning of their data has led to the following comparison.

Equatorial lowland rain forest, Guyana, Brazil (Belem), Ecuador, northern Peru $\bar{x} = 2.1 \pm 0.2$ (1-4) in 20
More southern Andean forest, Tingo Maria, Peru, 670 m, 9°6′S, and Buenavista, Bolivia, 500 m, 17°20′S $\bar{x} = 3.1 \pm 0.3$ (2-4) in 9

In the equable equatorial climate these snakes probably reproduce throughout the year; Zug et al. (1979) mentioned gravid females in February, April, June, September and December. Away from the equator in montane areas with more seasonal climate, reproduction is probably limited to the most favorable time of year, with larger clutches to compensate for their lesser frequency.

Elaphe guttata. Divided into northern and southern samples, the available records are as follows:

Northern (Maryland, Indiana) $\bar{x} = 13.5$ (3-30) in 30
Southern (Kansas, Tennessee, Texas, Florida) $\bar{x} = 13.2 \pm 2.0$ (4-28) in 12

No geographic trends are revealed by these figures. Most of the records are of clutches laid by captive snakes. Especially, the 20 clutches reported by Groves (1969) and 10 reported by Bechtel and Bechtel (1958, 1962) were of snakes in a captive colony, some second and third generation offspring from parents of different provenance. Bechtel and Bechtel (1958, 1962) found that their captive-reared young consistently reproduced as two-year-olds, but evidently they were maintained at high temperature with no hibernation, and it is doubt-

ful whether such early maturity could be attained under natural conditions.

Elaphe obsoleta. This large forest snake is widely distributed in the eastern United States, and many records of clutch size have been published but no large local series are available.

Northeastern (New York, Pennsylvania, Ohio, Indiana, Maryland, Kentucky, District of Columbia, West Virginia) $\bar{x} = 13.9 \pm 1.3$ (6-44) in 29

North-central (Kansas, Missouri) $\bar{x} = 11.2 \pm 1.1$ (6-27) in 25

Southern (South Carolina, Georgia, Oklahoma, Louisiana, Florida, Texas) $\bar{x} = 14.1 \pm 2.3$ (7-41) in 14

No clear trends are discernible.

Farancia abacura. Records of clutch size indicate that this is one of the most prolific of North American snakes, but the records are few and not well distributed to show geographic variation.

Eastern *(abacura)* $\bar{x} = 48.3 \pm 10.5$ (25-104) in 8

Western *(reinwardti)* $\bar{x} = 27.6 \pm 3.8$ (11-50) in 11

Heterodon nasicus. Inadequate material is available for comparing clutch size in different parts of the range, but there is little evidence of geographic variation.

Northern (Alberta, Manitoba, Minnesota, Montana) $\bar{x} = 8.9 \pm 1.0$ (5-12) in 7

Central and southern (Kansas, Missouri, Texas) $\bar{x} = 9.2 \pm 1.1$ (4-23) in 24

These figures provide no evidence of geographic change.

Heterodon platyrhinos. This wide-ranging snake is highly variable in clutch size, with a range at least from 4 to 61. However, geographic trends are not clear. Platt (1969) has summarized much of the literature. To study geographic trends he divided the range into northern, middle, and southern sections, and he made similar comparison of three longitudinal divisions. The following are derived from combining of Platt's "middle" and "southern" areas.

Northern (Minnesota, Wisconsin, New York, Ohio, Connecticut, Nebraska, Iowa, Illinois, Indiana, Ontario) $\bar{x} = 25.1$ in 20

Southern (Kansas, Oklahoma, Missouri, Maryland, South Carolina, Georgia, Florida) $\bar{x} = 20.6$ in 35

Thus it seems there is some tendency to increase clutch size northward, but Platt (op. cit.) obtained a slightly lower mean for his middle area (19.1) than for his southern area (22.1). Western, central and eastern divisions had similar means (21.4, 23.8 and 22.3, respectively).

Imantodes cenchoa. This tropical and arboreal colubrid ranges from Mexico through Central America and much of South America. Reproductive data have been assembled by Zug, Hedges and Sunkel (1979) and Duellman (1978). The records are here partitioned to compare clutch size in the snakes of the South American equatorial rain forests with those from more seasonal climates in Mexico and Central America. From the distribution of gravid females and hatchlings in the samples, Zug et al. (op. cit.) tentatively concluded that reproduction was continuous in the South American rain forests, but was confined to the long rainy season in the more northern samples.

Northern (Mexico, Honduras, Panama) $\bar{x} = 2.6 \pm 0.3$ (1-3) in 7

Southern (Ecuador, Peru) $\bar{x} = 1.7 \pm 0.2$ (1-3) in 18

Although the samples are small, there is indication of increased clutch size northward where reproduction may be seasonal.

Lampropeltis calligaster. Records of clutches are somewhat concentrated in Kansas and Missouri, but division of available records into northern and southern series seems to indicate latitudinal variation.

Northern (Kansas, Indiana; Illinios and Missouri except southern parts) $\bar{x} = 9.0$ (6-13) in 21

Southern (southern parts of Illinois and Missouri; Georgia, Oklahoma, Texas) $\bar{x} = 11.0$ (5-17) in 9

Northward decrease is suggested, but more substantial samples are needed.

Lampropeltis getulus. Records of clutch size in this transcontinental species are well scattered, but grouped in regional categories they seem to show both latitudinal and longitudinal variation.

Northern (Ohio, Illinois, Kansas, Kentucky) $\bar{x} = 10.6 \pm 0.6$ (6-14) in 15

Southeastern (Georgia, Florida, Louisiana, North Carolina, Oklahoma, Texas) $\bar{x} = 9.8 \pm 1.1$ (5-17) in 15

Southwestern (Arizona, southern California, New Mexico, Sonora) $\bar{x} = 4.9$ (2-9) in 48

Increase northward in clutch size is indicated. The separate samples from southern states, Georgia-Florida, Louisiana-Texas, and Arizona-California, all have means markedly lower than that for the northern group. Also, there is evidently a longitudinal trend, from smaller clutches in the southwest to larger in the southeast. The large southwestern sample is based entirely on snakes in a captive colony (Zweifel, 1980), some of which were second or third generation captives, and many were hybrids between subspecies. In 35 clutches laid by female hybrids having one parent of the subspecies *splendida* or *nigritus,* mean was 4.4 ±0.2 (2-7) eggs, whereas in 13 clutches of *L. g. californiae* mean was 6.3 ±0.7 (2-9) eggs. Hence it seems that the inland, desert-living *L. g. splendida* may have, on the average, smaller clutches than the coastal *L. g. californiae.*

Lampropeltis triangulum. This species is notable for its extensive geographic range, within which it undergoes striking changes in body size, color, pattern, habitat preferences and food habits. Doubtless there are parallel changes in reproductive strategies, but pertinent information is lacking for most populations. Clutch sizes in several populations are shown (Fig. 11) mostly from records of captive females kept or from published records compiled by Tryon and Murphy (1982). The large northeastern milk snakes, subspecies *triangulum,* seem to average about twice as many eggs per clutch as are found in other populations. It is not yet known whether there is corresponding increase in the large tropical representatives of the group.

Leptodeira annulata. This snake has an extensive range, from Mexico far into South America. Available samples indicate latitudinal change in size of clutch.

Northern (southern Mexico, Guatemala, El Salvador) $\bar{x}=8.2$ ±0.5 (6-10) in 10
Southern (Ecuador, Peru) $\bar{x}=4.1$ ±0.2 (2-7) in 36

The relatively small sample from the seasonal climates of Mexico and Central America averaged more than twice as many eggs as the large equatorial sample.

Micrurus fulvius. Through the recent studies of Quinn (1979) on the Texas coral snake and Jackson and Franz (1981) on the Florida population, geographic variation in clutch size in this species is suggested.

Florida *(fulvius)* $\bar{x}=7.4$ ±1.1 (3-13) in 9
Texas *(tenere)* $\bar{x}=5.9$ ±0.8 (3-9) in 7

These differences are proportional to mean lengths, SVL, of the adult females. For *fulvius* $\bar{x}=740$ mm; for *tenere* $\bar{x}=554$ mm.

Nerodia erythrogaster. The few available records, from scattered localities, suggest that litter size increases northward.

Northern (Ohio, Illinois, Missouri, Kansas) $\bar{x}=15.7$ ±1.4 (8-30) in 20
Southern (Oklahoma, Louisiana, Texas) $\bar{x}=12.0$ ±1.9 (4-22) in 10

Nerodia fasciata. Both large series and scattered records are available to show size of litter in the southern water snake.

Eastern (southeastern North Carolina and South Carolina) $\bar{x}=20.5$ in 97
Northwestern (Missouri and Arkansas) $\bar{x}=17.0$ ±3.1 (7-23) in 5
Southern (Gulf states) $\bar{x}=18.4$ ±1.2 (5-41) in 43

The North and South Carolina samples had similar means, 20.16 from North Carolina (Osgood, 1978) and 21 (2-50, N = 21) from the Savannah River Project, South Carolina. The Gulf state records were mostly from Louisiana and Florida, with a few from Texas and one from Mississippi. Slight increase in size of litter from south to north may be indicated.

Better evidence of geographic variation was obtained by comparing more localized samples; in 9 Florida snakes of the subspecies *compressicauda* and *pictiventris* litters averaged 20.0 ±3.7 (5-57), whereas in 22 Louisiana *confluens* average was 16.5 ±1.0 (11-27). There may be an increase in litter size from inland populations to those of coastal areas.

Nerodia rhombifera. Litters of this large water snake vary widely in numbers of young, depending on size of the female, and probably upon food supply. Evidence for geographic variation in litter size is not fully convincing.

Northern (Illinois, Missouri, Kansas) $\bar{x}=28.8$ ±2.1 (23-34) in 5
Central (southeastern Missouri) $\bar{x}=37.1$ ±1.9 (27-56) in 20
Central (western Tennessee, Reelfoot Lake) $\bar{x}=27.1$ ±2.1 (13-42) in 18
Southern (Oklahoma, Texas, Louisiana) $\bar{x}=29.3$ ±5.4 (14-62) in 10

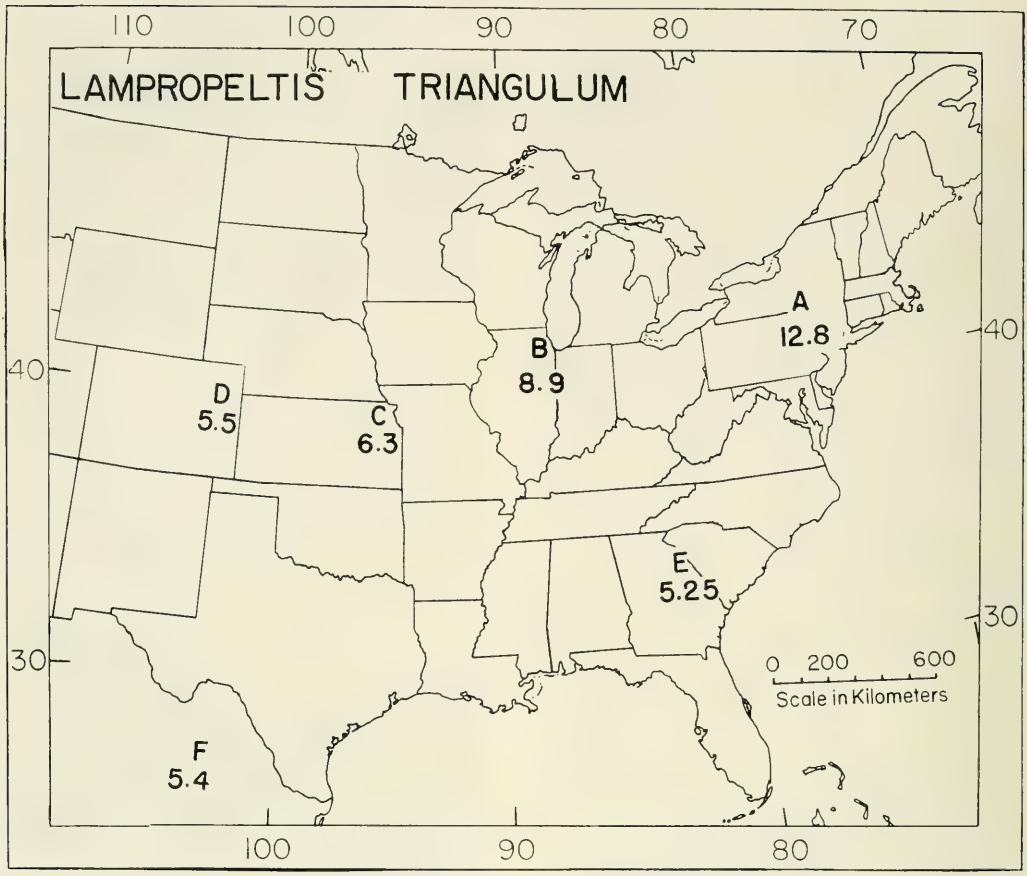

FIG. 11.—Map showing geographic variation in clutch size in *Lampropeltis triangulum.* A. NE United States *(triangulum)* **12.8** ±1.0 (6-24) in 27; B. NE Illinois *(triangulum)* **8.9** (5-11) in 9; C. E Kansas and neighboring areas *(syspila)* **6.3** (3-9) in 17; D. Nebraska, Colorado *(gentilis)* **5.5** ±0.7 (4-12) in 8; E. SE United States *(elapsoides)* **5.25** ±0.4 (4-7) in 8; F. Texas, Mexico, Central America (*annulatum, arcifera, hondurensis, nelsoni,* ssp.) **5.4** ±0.35 (3-9) in 25.

The sample from "southeastern Missouri," reported by Betz (1963), included several females from La Place, Louisiana, and therefore is not well suited to show geographic variation. Furthermore, there may have been some selection for large females in Betz's study, resulting in the high mean for litter size in his sample. The southeastern Missouri and western Tennessee samples are so near together that the difference in their means could scarcely have much geographic significance.

Nerodia sipedon. Many samples both local and composite are available and indicate extensive geographic variation (Fig. 12). Geographical trends are not clear. In a population study in southeastern Michigan, Feaver (1977) found a mean of only 11.8 young per litter, but he did not indicate his sample size. Presumably it was small, and perhaps weighted to primiparous females, as all other samples, including those in the general region of Feaver's study, have markedly higher means. Most samples have means with about 20 young. A puzzling exception is the mean of 29.9 found by Baumann and Metter (1977) in a sample from central Missouri, since other series from eastern Missouri and from Kansas had markedly lower numbers. Bauman and Metter's series was collected in the vicinity of a fish hatchery, where the snakes were abundant and presumably well fed. Perhaps the surplus of food rendered the snakes of this population unusually productive.

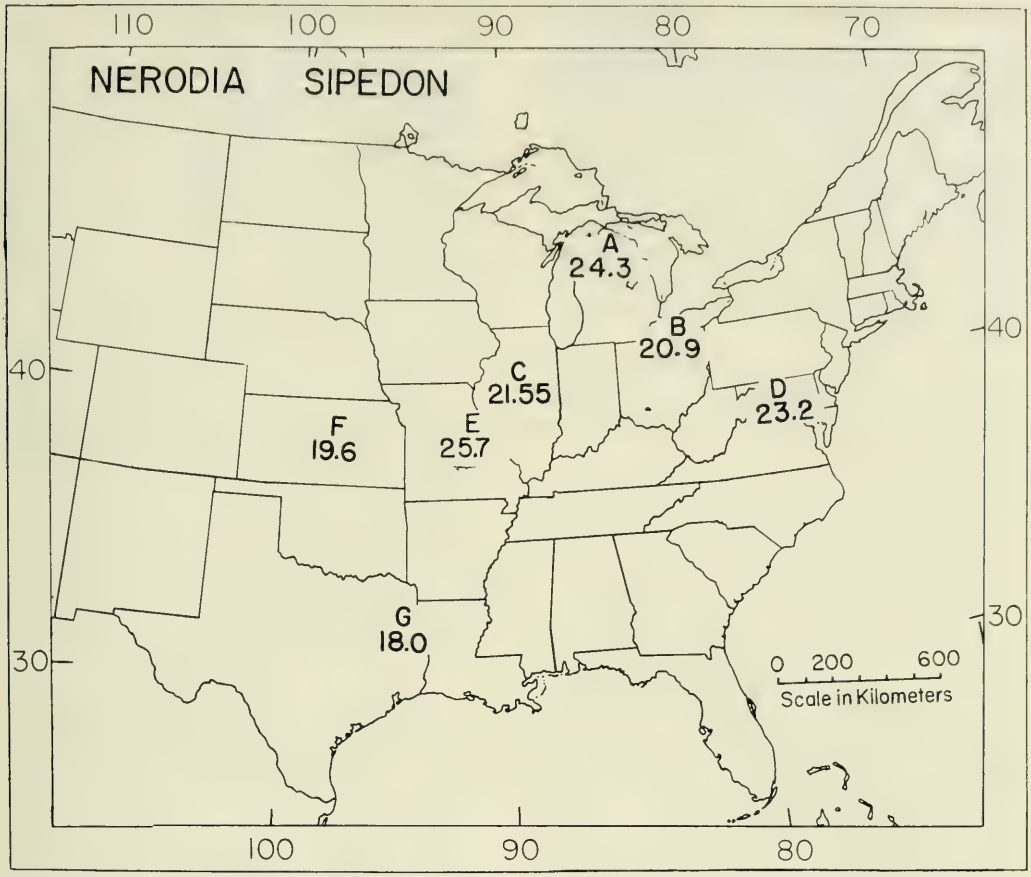

FIG. 12.—Map showing geographic variation in litter size in *Nerodia sipedon.* A. N Michigan *(sipedon)* **24.3** ±3.1 (15-45) in 9; B. Lake Erie islands *(insularum)* **20.9** ±1.6 (6-34) in 23; C. Illinois *(sipedon)* **21.55** ±4.8 (8-51) in 10; D. Maryland and Ohio *(sipedon)* **23.2** ±2.3 (11-35) in 19; E. Missouri *(sipedon)* **25.7** (9-66) in 95; F. Kansas and Iowa *(sipedon)* **19.6** ±2.8 (7-39) in 14; G. Tennessee and Texas *(sipedon* and *pleuralis)* **18.0** ±2.6 (7-35) in 9.

Aldridge (1982) studying a population in east-central Missouri, found a high degree of correlation between female size and number of embryos, but at an earlier stage of development, such correlation was lacking between female size and number of yolked follicles. Ordinarily, in each female several follicles underwent atresia, and presumably such losses were greater in the smaller females.

Nerodia taxispilota. Two substantial series are available to show size of litter in different parts of the range.

Northern (Virginia, Chesterfield County)
$\bar{x}=33.9$ (19-63) in 23
Southern (South Carolina, Savannah River)
$\bar{x}=28$ (7-63) in 51

Northward increase is suggested.

Opheodrys aestivus. The several samples available for this small arboreal snake seem to indicate geographic variation in its small clutch.

Northeastern (Ohio, Maryland, northeastern Kentucky, North Carolina)
$\bar{x}=5.3$ ±0.4 (4-9) in 18
Northwestern (Kansas, Missouri, Illinois, northwestern Kentucky)
$\bar{x}=6.2$ ±1.0 (4-10) in 5
Central (northern Arkansas)
$\bar{x}=6.1$ ±0.2 (3-10) in 77
West-central (Oklahoma)
$\bar{x}=5.6$ ±0.4 (3-8) in 16
Southwestern (southern Louisiana, eastern Texas) $\bar{x}=5.1$ (1-10) in 36

A northward increase is indicated, at least in the western part of the range. The southwestern sample is mainly from Tinkle (1960) who found a mean of 4.7 (1-9) winter

follicles larger than 5 mm in diameter in a series of 30 females from southern Louisiana. He equated these enlarging winter follicles with clutches that the snakes would have laid the following summer. A Texas clutch of 12 eggs recorded by Sabath and Worthington (1959) is excluded here since it may have been a composite. Palmer and Braswell (1976) reported a communal nest with 74 eggs in the insulating material of a discarded refrigerator in oak woodland in North Carolina.

Opheodrys vernalis. The three samples with extensive series suggest that clutches increase in number of eggs from south to north.

Quebec and Ontario, 47°N
$\bar{x} = 7.5$ (4-10) in 19
Northern Michigan, 45°N
$\bar{x} = 6.7 \pm 0.2$ in 53
Chicago area, 42°N
$\bar{x} = 5.8 \pm 0.4$ (5-15) in 25

Five clutches from the northwestern part of the range (Manitoba, South Dakota), however, average 5.4 (4-8), while seven clutches from the southern parts of the range (Ohio, southern Illinois, Virginia, Missouri, Texas) average 10.1 (2-18), with three Illinois clutches each having 18 eggs.

Pituophis melanoleucus. This is a transcontinental species, but ecologically its populations fall into three fairly distinct units, the eastern pine snakes, the Great Plains bull snake, and the far western gopher snakes, each formerly allocated as a separate species. They differ in clutch size, as shown by the following figures.

Eastern United States $\bar{x} = 6.8$ (6-13) in 40
Great Plains $\bar{x} = 12.9$ (5-22) in 38
Great Basin (northern Utah)
$\bar{x} = 8.4$ (4-15) in 19
West Coast $\bar{x} = 8.5$ (3-19) in 33

Seemingly, clutch size is highest at midcontinent with reduction in numbers toward both coasts. It is not clear whether there is also a latitudinal change. In western Nebraska, Imler (1945) found a mean of 12.8 eggs in 22 females. Sixteen others from scattered localities in North Dakota, Kansas, Missouri and Oklahoma averaged 13.1. On the East Coast, five records of the southern *mugitus* averaged 5.8, whereas 35 of the northern *melanoleucus* (mostly from captives in the San Diego Zoo) averaged 6.7 eggs. On the West Coast 25 records of the desert subspecies, mainly from southern California, averaged 8.1, whereas seven records of the northern *catenifer* averaged 9.3 eggs. Slight decrease from north to south is suggested in both instances.

Regina grahami. One local series and a few scattered records are available to indicate litter size in this small crayfish-eating watersnake.

Northern (Kansas, Missouri, Illinois, Iowa)
$\bar{x} = 16.4$ (4-39) in 24
Southern (Louisiana, Texas)
$\bar{x} = 12.2 \pm 2.3$ (6-19) in 6

Southward reduction in litter size is suggested by the figures, but more records from the southern part of the range are needed to demonstrate this.

Regina septemvittata. Two samples, one small and the other a composite, are available for this second small species of crayfish-eating watersnake.

Northern (Pennsylvania, Michigan, Ohio, Indiana, Illinois)
$\bar{x} = 9.3 \pm 0.6$ (6-14) in 18
Southern (Kentucky, Virginia, Georgia, North Carolina) $\bar{x} = 12.2$ (8-17) in 13

Northward reduction in litter size is suggested.

Sistrurus catenatus. The five available samples of litter size indicate possible differences over the range.

Northeastern (Pennsylvania)
$\bar{x} = 6.7 \pm 0.5$ (3-9) in 12
North-central (Ohio, Indiana, southern Michigan, Illinois)
$\bar{x} = 7.9 \pm 0.7$ (5-13) in 15
Northwestern (Wisconsin, Buffalo County)
$\bar{x} = 11.7$ in 58
Western (northwestern Missouri, Holt County) $\bar{x} = 6.3$ (5-10) in 17
Southwestern (Kansas, Oklahoma, Texas)
$\bar{x} = 5.9 \pm 0.7$ (3-11) in 13

Seemingly there is increase both from east to west and from south to north.

Sistrurus miliarius. A sample is available for each of three subspecies of pigmy rattlesnakes, and north-south geographic variation is suggested.

Carolinas *(miliarius)*
$\bar{x} = 5.2 \pm 0.3$ (3-7) in 16
Texas *(streckeri)* $\bar{x} = 8.6 \pm 2.8$ (3-32) in 9
Florida *(barbouri)* $\bar{x} = 7.4$ (2-18) in 18

The mean for the Texas sample is raised by one remarkably large litter of 32. Small litter

size is associated with relatively small body size in the northern subspecies, *S. m. miliarius*.

Storeria dekayi. This small, secretive, viviparous natricine occurs from southern Canada to northern Mexico in eastern North America. Two local samples of clutch sizes in widely separated parts of the range suggest that geographic variation is minimal. In a sample of 14 females from Long Island, Clausen (1936) found a mean of 14.6 ±0.8 (9-20) young. In southern Louisiana, Kofron (1979) found 14.9 young in 30 females. Mean litter sizes over much of the range are shown on Figure 13. Although the lowest means are from the southern parts of the range (Florida, Texas, Oklahoma), this is not a consistent trend, as the Louisiana mean is high. Slight increase from west to east is indicated.

Storeria occipitomaculata. Several samples of the red-bellied snake, of varying size and homogeneity, are available to show litter size.

Northeastern (Quebec, Connecticut, Ohio, Maryland, Indiana)
$\bar{x}$ = 8.2 (3-15) in 11

Northeastern (New York)
$\bar{x}$ = 7.8 (6-14) in 14

North-central (northern Michigan)
$\bar{x}$ = 7.2 (1-15) in 84

Northwestern (Minnesota)
$\bar{x}$ = 9.7 (3-18) in 11

Southeastern (South Carolina)
$\bar{x}$ = 9.0 (2-15) in 31

Geographic trends are not clearly indicated by these figures. In the South Carolina

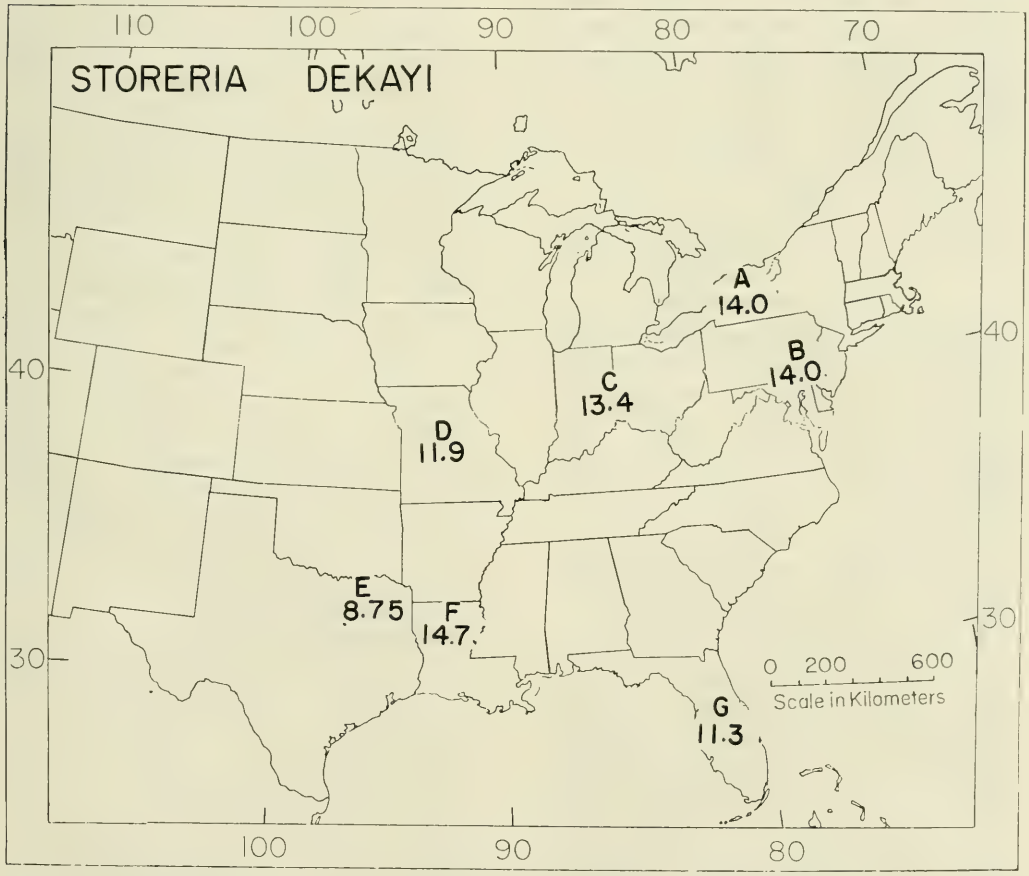

FIG. 13.—Map showing geographic variation in litter size in *Storeria dekayi*. A. Ontario, New York **14.0** ±0.7 (5-21) in 33; B. Maryland, New Jersey **14.0** ±3.0 (3-27) in 9; C. Indiana, Ohio **13.4** ±1.8 (6-23) in 10; D. Kansas, Missouri, Illinois **11.9** ±1.0 (3-24) in 35; E. Oklahoma, Texas **8.75** ±1.1 (3-12) in 8; F. Tennessee, Louisiana **14.73** (5-17) in 37; G. Florida (and Alabama, 1) **11.3** (6-31) in 16.

population, studied by Semlitsch and Moran (1984), adult size averages only about 81% of that in the Michigan population studied by Blanchard (1937). South Carolina neonates were found to average 61 mm SVL, contrasted with 72 mm in Michigan. Nevertheless, South Carolina neonates are relatively larger, compared with parental size, thus "reproductive effort" is greater in the more southern population.

Tantilla gracilis. Twelve Kansas females (KU) average 1.75 ova (2 in 7, 1 in 4, 3 in 1). In large series in Oklahoma, Force (1935) found that there were usually either 2 or 3 eggs per clutch. Seemingly clutch size increases southward.

Thamnophis butleri and T. brachystoma. These two allopatric northeastern garter snakes are closely related dwarfed relatives of *T. radix.* Their ranges are within areas of Pleistocene glaciation, and the longitudinal range is not great. *T. brachystoma* is the more dwarfed and specialized in lepidosis.

Southeastern Michigan *(butleri)*
$\bar{x} = 11.3$ (6-20) in 32
Northern Ohio *(butleri)*
$\bar{x} = 8.2 \pm 1.6$ (4-14) in 5
Southwestern New York *(brachystoma)*
$\bar{x} = 7.2$ (3-12) in 17

Ford and Killebrew (1983) who reported upon the Michigan sample, noted that neonate size was positively correlated with female size, but negatively correlated with litter size, but that *relative clutch mass* did not change with female size. Pisani and Bothner (1970) found evidence of a biennial reproductive cycle in *T. brachystoma.* Carpenter's (1952) findings concerning *T. butleri* in Michigan suggests that females of this species also produce litters only in alternate years or even less frequently.

Thamnophis elegans. Although samples are lacking from major portions of the geographic range, those samples that are available indicate that significant geographic variation in litter size occurs. The wide-ranging subspecies *vagrans* of the Great Basin and Rocky Mountain region is generalized in habits, partly aquatic and partly terrestrial, in contrast with the mesic-terrestrial subspecies *terrestris* of the coastal region, and with the subspecies *elegans* found in dry-terrestrial habitats, except in northeastern California (Lassen and Modoc counties). There it becomes partially aquatic, tending toward the highly aquatic *biscutatus* of the Klamath Lakes basin. In the Puget Sound region, *nigrescens* is like *vagrans,* but smaller and darker.

As shown on the map (Fig. 14), litter size is greatest in southern *terrestris* and in Great Basin *vagrans,* with notable reduction to the northwest in Puget Sound *nigrescens,* and to the west, in *terrestris* of northwestern California. In *terrestris* of the northern California coast there is notable north-to-south decrease in litter size. The *vagrans* sample was a composite of scattered records, 2 from British Columbia, 6 from Idaho, 3 from Nevada, 2 from Utah, 1 from Colorado and 3 from New Mexico, but there may be much variation within the range of this subspecies.

Thamnophis errans, a dwarfed terrestrial garter snake of northwestern Mexico, is an obvious isolated derivative of *T. elegans* and of its subspecies *vagrans,* and has often been included with *elegans* despite the morphological and geographical hiatus separating them. Litter size in a *T. errans* sample (N = 7) averaged 7.9 (Fig. 14), fewer than in any *T. elegans.*

Thamnophis marcianus. This garter snake is confined to the desert southwest in the United States, but ranges southward into the tropics through much of Mexico and Central America. In a preliminary report on the species' geographic variation in reproductive cycles and strategies, Karges (1982) compared the populations of the four main physiographic regions of the range. He found that the most northern population differed from the other three in having females mature at larger body size, and having litters averaging more young.

Thamnophis ordinoides. Three samples are available to show litter size in this small terrestrial garter snake of western Oregon and Washington, and northwestern California.

Northern (Puget Sound) $\bar{x} = 8.6$ (3-15) in 53
Inland (Willamette Valley)
$\bar{x} = 10.5$ (3-20) in 16
Southern (Del Norte County, California)
$\bar{x} = 6.4$ (4-8) in 18

These figures suggest reduction from inland to coastal localities, and on the coast reduction from north to south. At the south-

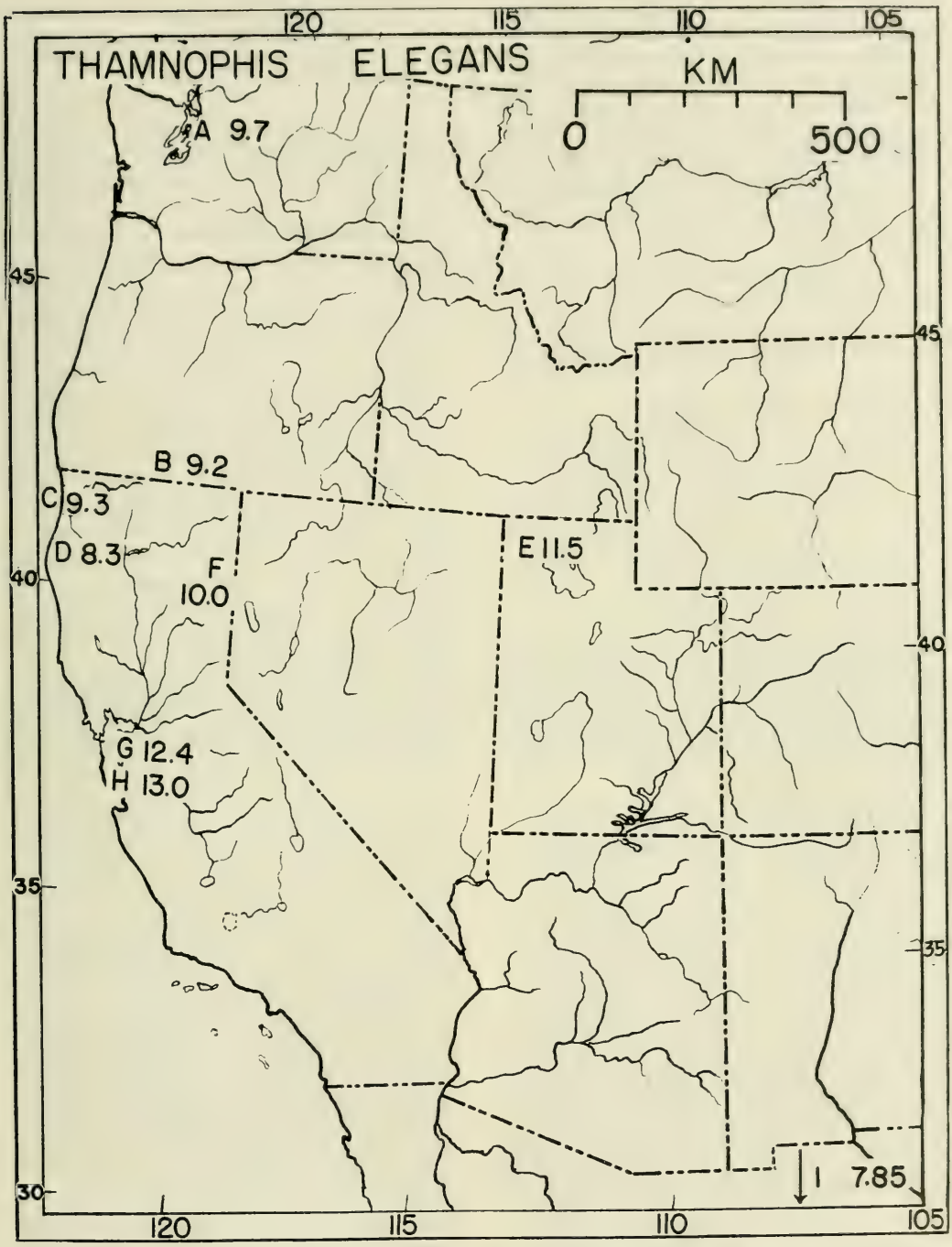

FIG. 14.—Map showing geographic variation in litter size in *Thamnophis elegans*. A. NW Washington, Puget Sound region *(nigrescens)* **9.7** (9-19) in 28; B. S-central Oregon *(biscutatus)* **9.2** (8-10) in 6; C. NW California coast, Del Norte County *(terrestris)* **9.3** in 17; D. NW California, Humboldt County *(terrestris)* **8.3** in 56; E. northern Great Basin *(vagrans)* **11.5** ±0.9 (4-20) in 17; F. NE California, Lassen County *(elegans)* **10.0** in 68; G. California coast, San Francisco vicinity *(terrestris)* **12.4** in 11; H. California coast, Santa Cruz *(terrestris)* **13.0** in 15; I. NW Mexico, Chihuahua, Durango *(errans)* **7.85** (6-10) in 7.

ern end of its range *ordinoides* is sympatric with the similar but larger *Thamnophis elegans terrestris* and *ordinoides* seems to average smaller in this area than elsewhere. The low mean litter size of 6.4 found in Del Norte County, California, is correlated with small body size of *ordinoides* in that area.

In the Puget Sound region Hebard (1951) found one-third of the adult females to be nonreproductive.

Thamnophis proximus. Many small series and isolated records are combined to yield four latitudinal samples, only one of which is adequately large in number of litters.

Northeastern (Indiana, Illinois)
$\bar{x} = 9.4 \pm 1.5$ (6-20) in 7
Northwestern (Kansas; one each in Nebraska and Missouri)
$\bar{x} = 12.4 \pm 1.4$ (6-28) in 14
Central (Oklahoma, Texas, Louisiana)
$\bar{x} = 11.6 \pm 0.7$ (4-24) in 41
Southern (Mexico, Nuevo Leon)
$\bar{x} = 10.0 \pm 0.8$ (8-13) in 5

No consistent trend is evident.

Thamnophis radix. The many records of litters available for this garter snake show much variation, part of it geographic, part of it based on size (and age) of female and part of it due to year to year changes and changing weather and food supply.

Northern (northern Illinois) $\bar{x} = 13.3$ in 43
Southern (northwestern Missouri, Holt County) $\bar{x} = 9.9$ in 47
Western (Nebraska, Kansas, Colorado)
$\bar{x} = 20.6$ in 16

The Missouri sample averaged 9.0 in 1980 but increased to 11.9 in 1982. In the Chicago area Cieslak (1945) found an average of 15.4 embryos in 1937–38 but there was decrease to 12.4 in 1941–42. In Douglas County, Nebraska, Lesch and Fawcett (1978) found an average of 19 embryos in females of more than 500 mm SVL, and 7.3 in females of less than 500. The difference in litter size between years in the Missouri sample was not due primarily to difference in female size. When correction for female body size by ANCOVA was made, adjusted means for 1980 and 1982 were 9.2 and 11.2 respectively.

Thamnophis sauritus. Available samples of litter size in this snake seem to show significant geographic variation.

Northern (northeastern and east-central states; *sauritus*)
$\bar{x} = 8.9 \pm 0.7$ (3-20) in 35
Southern (Florida; *sackeni*)
$\bar{x} = 16.9 \pm 2.3$ (8-26) in 8

Means, minima and maxima are substantially higher for the Florida litters *(sackeni)* than for the litters from the northern states *(sauritus).*

Thamnophis sirtalis. As a transcontinental species this snake is subject to much variation in litter size (Fig. 15). Geographic trends are somewhat obscured by the great variation between individuals in number of young per litter. Number of young is positively correlated with size of female. In various parts of the range occasional females are found that greatly exceed the usual size, and such individuals may produce exceedingly large litters (72, 74, 78, 80 and 85 have been recorded). Such litters, reported upon because the author was impressed with the large number, are excluded from my calculations of regional averages, because they would introduce bias, making the means unnaturally high.

It appears that litters average largest in the eastern subspecies *sirtalis,* at about latitude 40°N, Ohio and the neighboring states to the east and west. From this area of maximum litter size there are gradients to the northeast, south and west, with smallest litters occurring in northern New England *(pallidula)* and on the West Coast *(infernalis, fitchi).* On the West Coast, in the Great Plains, and on the East Coast there is some reduction in litter size in the northernmost populations sampled. However, the main trend seems to be from maximum litter size in the most mesic central part of the range (where conditions are probably nearest the ecological optimum) to smaller litters in outlying regions where conditions are unfavorably xeric or are subject to extremes of low or high temperatures.

Table 4 shows 14 samples of litter size in local samples, widely distributed over the range of the species. Most of these were combined with other records to obtain the figures used in the map. An unresolved problem is why in Hoffman's and Pisani and Bothner's samples from New York ($\bar{x} = 18.2$ and 14.0) litter size was so much smaller than in other series from that state (25.9 and

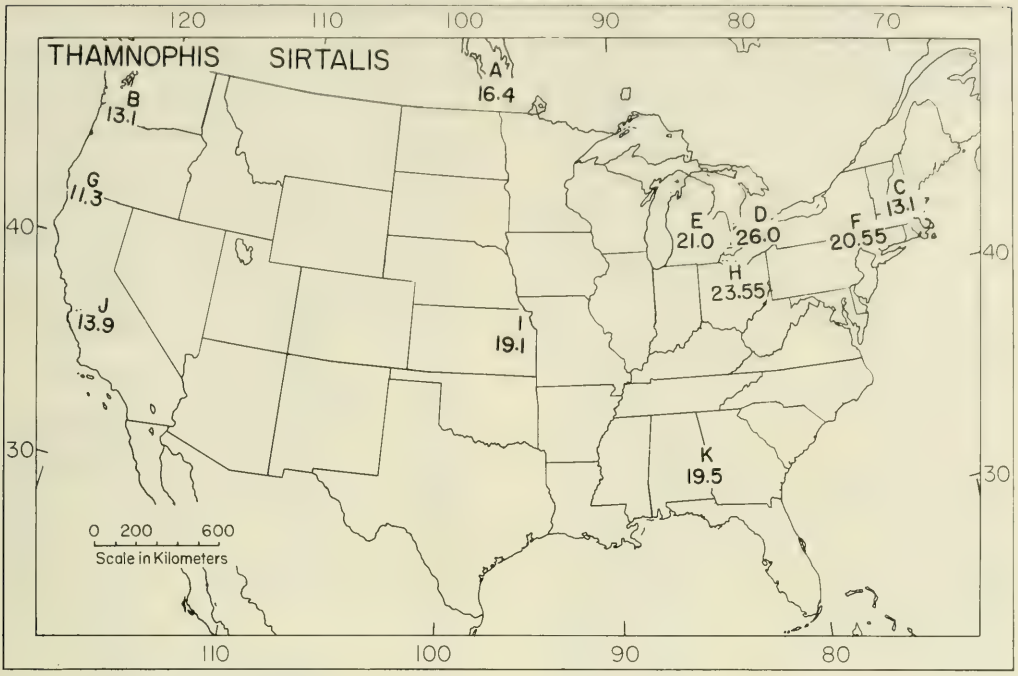

FIG. 15.—Map showing geographic variation in litter size in *Thamnophis sirtalis*. A. Manitoba, interlake region *(parietalis)* **16.4** ±1.4 in 14; B. W Washington and W Oregon *(concinnus)* **13.1** (5-29) in 11; C. New Hampshire *(pallidula)* **13.1** ±0.6 (9-27) in 113; D. Ontario *(sirtalis)* **26.0** in 31; E. Michigan *(sirtalis)* **21.0** (13-32) in 58; F. New York *(sirtalis)* **20.55** (7-51) in 61; G. SW Oregon, NW California *(fitchi)* **11.3** ±1.0 (5-23) in 22; H. Indiana, Ohio, Maryland, Pennsylvania *(sirtalis)* **23.55** ±2.41 (8-57) in 44; I. NE Kansas **19.1** ±1.3 (9-42) in 34; J. California *(fitchi* and *infernalis)* **13.9** ±3.0 (4-52) in 16; K. Florida, Kentucky, Louisiana *(sirtalis)* **19.5** (9-38) in 18.

20.1 respectively). In my sample from the University of Kansas Natural History Reservation there was much variation in means from year to year, and weather seemed to be the controlling factor. However, method of sampling also may have affected results. Counts of litters born in captivity averaged higher than embryo counts obtained from palpating females. The females that were repeatedly subjected to palpation tended to have fewer embryos each time and evidently mortality of embryos resulted even though the snakes were gently handled. Secondly, as indicated by Stewart (1968) embryo counts by palpation are difficult, and may tend to err on the low side, when litters are large and embryos are crowded together.

The investigators who have reported litter sizes in *Thamnophis sirtalis* have had a variety of interests, but none has been concerned with geographic variation. In some instances persons desiring litters of garter snakes for study probably have collected and kept every gravid female that could be found thus obtaining a random sample, but in other instances where large numbers of young were wanted, smaller females and those relatively little distended by embryos may have been discarded in favor of larger and more obviously gravid females. It is not surprising that Blanchard and Blanchard's (1941) Michigan sample had a mean (23.2) larger than Carpenter's (1952) mean of 18.0, because the Blanchards' sample was based on experimental captive females that may have been selected for size originally, and in some instances were kept for several successive years and were well fed and well adjusted to captivity.

In 1982 I collected series in southwestern Oregon and northwestern California, one sample near sea level and another at 1350-1700 m, to determine the effect of altitude on litter size. The difference turned out to be small and inconclusive.

TABLE 4. Local samples of litter size in *Thamnophis sirtalis*

$\bar{x}$	N	Place	Subspecies	Authority	Remarks
12.9 ±0.60	104	New Hampshire, Hanover	*pallidula*	Zehr 1962	embryos dissected
15.1 (9-27)	9	New Hampshire, Hanover	*pallidula*	Zehr 1962	litters born
18.2 (6-34)	42	New York, Ithaca	*sirtalis*	Hoffman 1970	litters born (15.8 normal yg. per litter)
14.0	14	New York, Olean	*sirtalis*	Pisani and Bothner 1970	embryos dissected
25.0	14	Ontario	*sirtalis*	Evans and Roecker 1951	litters born
29.0 (12-49)	7	Ontario	*sirtalis*	Logier 1929, 1930	litters born
18.0	20	Michigan, Ann Arbor	*sirtalis*	Carpenter 1952	litters born
15.5	7	Kentucky, Harlan County	*sirtalis*	Barbour 1950	litters born
16.43 ±1.43 (7-25)	14	Manitoba, Interlake region	*parietalis*	Gregory 1977	embryos
19.15 ±1.26 (12-42)	34	Kansas, Douglas County	*parietalis*	Fitch MS	litters born
20.0 ±1.91 (9-39)	20	Kansas, statewide	*parietalis*	Fitch MS	embryos dissected
14.72 ±0.54 (4-29)	95	Kansas, Douglas County	*parietalis*	Fitch MS Fitch 1965	embryos palpated
11.3 (5-29)	7	Oregon, Corvallis	*concinnus*	Stewart 1968	litters born
11.32 ±0.98 (5-23)	22	SW Oregon NW California	*fitchi*	Fitch MS	embryos dissected

High altitude sample
$\bar{x} = 12.2 \pm 1.8$ (6-23) in 11
Low altitude sample
$\bar{x} = 10.5 \pm 0.8$ (5-14) in 11

Tropidoclonion lineatum. Anderson's (1965) statement that litters averaged 6 (3-12) evidently was based on Missouri material, but he did not indicate sample size. Five Kansas females (KU) also averaged 6.0 ±1.3 (3, 3, 6, 7, 11). For 16 other litters, reported in the literature from Texas and Oklahoma, mean was 7.3 ±0.7 (2-12) suggesting the possibility that litter size increases southward.

Virginia striatula. Litters are small in this small, terrestrial natricine. One local series and various scattered records are available to show trends.

Northern (North Carolina, Missouri, Oklahoma) $\bar{x} = 5.2 \pm 0.4$ (2-7) in 15
Southern (Texas) $\bar{x} = 5.0 \pm 0.3$ (2-9) in 37

The records suggest that litter size is remarkably constant throughout the range.

Virginia valeriae. Records of births in this diminutive and secretive natricine are most concentrated in the region of southern Pennsylvania and Maryland, and therefore are not well suited to demonstrate geographic variation. The small latitudinal difference indicated by the following figures weakly suggest increased litter size northward.

Northern (Pennsylvania, Ohio)
$\bar{x} = 6.9$ (5-14) in 19
Southern (Maryland, Illinois, Kentucky, Missouri, Tennessee, Mississippi)
$\bar{x} = 6.1 \pm 0.6$ (4-14) in 22

CROCODILIANS

Crocodilian reproduction is influenced by the large size of these reptiles, and their oviparity, polygyny with relatively large males, partly aquatic habits, tropical (to warm-temperate) distribution, and maternal tending of nests and hatchlings. Many years are required to attain maturity. Insofar as known for each species, there is a fairly short annual breeding season, with a single clutch of many eggs.

Alligator mississippiensis. Several geographic samples of clutch size in the American alligator are available, but these do not represent much latitudinal spread.

Southeastern Georgia, Okefinokee Swamp $\bar{x} = 30$ (12-44) in 55
North-central Florida (Dietz and Hines, 1980) $\bar{x} = 37.5 \pm 1.4$ in 67
North-central Florida (Goodwin and Marion, 1978) $\bar{x} = 30.3 \pm 2.6$ (1-39) in 14
Southwestern Louisiana $\bar{x} = 38.9$ (2-58) in 315
Southern Florida, Everglades $\bar{x} = 33.1$

All but the Everglades sample were from near 32°N. It is suspected that the differences between the samples resulted from differences in food supply, and from density and age structure of the population, rather than from geographic divergence. Joanen (1969) who studied the Louisiana population, found no correlation between body size of female and clutch size.

Caiman crocodilus. Occurring from Mexico through the Central and South American tropics into the Temperate Zone in the southern hemisphere, the caiman is subject to much geographic variation. Figures presented by Brazaitis (1973) suggest that the more northern *C. c. crocodilus*, compared with *C. c. yacare*, is smaller and produces fewer eggs per clutch, "15-40" vs "30-45." The two local samples and one composite sample that are available support this suggestion.

Central Bolivia, about 16°S *(yacare)* $\bar{x} = 33$ (23-41) in 37
Venezuelan llanos, about 8°N *(crocodilus)* $\bar{x} = 29.0$ (17-38) in 200
Colombia, Peru, equatorial, 11°N to 10°S *(crocodilus, fuscus, apaporiensis)* $\bar{x} = 23.3$ (10-21) in 20

Crocodylus acutus. The American crocodile has an extensive geographic range, encompassing varied tropical habitats and climates.

Southern Florida, 25°N $\bar{x} = 44$ (15-81)
Hispaniola, Dominican Republic, Enriquillo Lake, 18°30′N $\bar{x} = 23.8$ in 80

Nesting at Enriquillo Lake occurs from mid-February to early April, but is delayed until several weeks later in the more seasonal climate of southern Florida. The relatively small clutch of the insular population follows a widespread trend. On the mainland the raccoon *(Procyon lotor)* is a major predator on nests, but such mammalian predators are absent on Hispaniola and most other Antillean islands, and probably predator pressure is much decreased as a result.

DISCUSSION AND CONCLUSIONS

Data have been presented above for every species of American reptile for which two or more geographic samples of clutch or litter size could be obtained. Obviously, differences between the compared samples were not always or entirely based on geographic variation. In many instances samples were small and differences in their means could have been due solely to chance. In other instances, including some large samples, important differences were apparent, but could have been due to the influence of special local or temporal conditions in either augmenting or counteracting geographic effects. The drastic results of drought in reducing egg production have been noted in *Cnemidophorus sexlineatus, C. tigris, Sauromalus obesus, Sceloporus merriami, Urosaurus ornatus* and *Uta stansburiana.* Year to year fluctuations in clutch size seem to be common. Comparably, major effects have been demonstrated in local habitats acting on neighboring populations of *Chrysemys picta, Pseudemys scripta* and *Basiliscus basiliscus,* causing them to differ from each other as much as geographically remote populations. In other species such effects may have distorted the geographic trends. Unfortunately, for most species geographic variation in clutch or litter size cannot be distinguished from other types of variation with the information currently available. In nearly every instance in which geographic samples are sufficiently large and well distributed to rule out the effects of other variables, it can be shown that geographic variation in clutch and litter size does indeed exist. Hence, in each species account all available geographic samples are presented as possible or partial examples of geographic variation, but with the realization that there is bias from nongeographic

factors in many of them. The large number of species sampled should reveal some major geographic trends, even with varying amounts of bias distorting many of the figures. However, the records assembled here will perhaps have their main usefulness as a starting point for future studies.

Subject to these qualifications some limited comments and conclusions are in order. All but five of the 137 species of American turtles, lizards, snakes and crocodilians investigated showed possible evidence of geographic variation in clutch or litter size. Presumably each species has tended through natural selection to evolve the clutch or litter size optimum for its survival. Production must be sufficient to compensate for normal mortality factors, but overproduction can be disadvantageous, and is presumably sometimes selected against in various ways. For instance burdening of the gravid female might render her more vulnerable to predation, shortening her life expectancy drastically; similarly increase in number of young, if achieved by compensatory reduction in their size, might make them available as prey to additional sets of small predators capable of decimating their numbers.

Size of clutch or litter is regarded as an attribute that populations have evolved through time in adaptation to their general environment and their ecological niche within that framework. The populations of wide-ranging species are especially subject to different sorts of selective pressures in different geographical areas, and through natural selection would tend to develop different clutch or litter sizes in different regions. Often such differences have genetic bases. In some cases adaptation conceivably could involve programming for optimal reproductive responses to different environmental forces, so that clutch could be adjusted and made either larger or smaller as appropriate for best survival of offspring and/or parent. In most instances I think the observable geographic differences in reproductive traits between populations result from a combination of genetic characters and direct responses of the individual to environmental effects.

Each of the wide-ranging species with which this report is concerned occurs in diverse biotic communities and is subject to different sets of selective factors in different parts of its range, so it should not be surprising if clutch size is subject to geographic variation. Doubtless many biotic and physical factors are involved in the selection for optimum clutch size in any species in a given area.

In contrast to the meager information available concerning clutch and litter size and their geographic variation in reptiles, much more attention has been devoted to the subject in birds and mammals (Rensch, 1934; Lack, 1966; Cody, 1966). A trend toward larger clutches and litters at higher latitudes was demonstrated by Rensch (1934), but there still is not complete agreement on the factors involved. Theories concerning the selection of clutch size in birds and litter size in mammals are largely concerned with the number of dependent offspring that the female parent (or pair) can feed successfully under various conditions. In reptiles (other than crocodilians), on the contrary, the neonates and hatchlings are independent from the beginning. After oviposition or parturition the female is not handicapped by maternal responsibilities but is free to reproduce again, and her death or survival does not directly affect the survival of eggs already laid or young born.

From analysis of factors that control clutch size in birds, Cody (1966) concluded that instability of environmental conditions is correlated with increased clutch size. Environments that are relatively stable climatically include those of the tropics, of oceanic islands, and of coastal regions. In each of these situations Cody found a trend of intraspecific reduction in clutch sizes. Under unstable conditions the risks encountered during development are greater and mortality is generally higher. The principle should apply to reptiles just as well as to birds. Partial support for this idea is provided by tables 5 and 6 showing decrease in clutch on islands and in relatively aseasonal tropical climates, but no trend of reduction from inland to coastal areas could be found.

Stearns (1976) and Ballinger (1978) have recently reviewed the literature and discussed ideas concerning clutch and litter sizes in vertebrates. Some factors that ob-

viously might affect size of brood through compensatory evolutionary adjustments are: age-specific mortality rates and life expectancy of adult female, frequency of brood production by the individual female; age at maturity in both male and female; usual size of hatchling or neonate; time, energy and risk invested in parental care; stability of environment; level of predation; and foraging- and escape-strategies of the species. As an example of this last factor, a heavy burden of eggs or embryos can be less well

TABLE 5. Changes in clutch and litter sizes from islands to adjacent mainland

Species	Island	Decrease, mainland to island	Mean no. of eggs or young in clutch or litter: island vs mainland		N = broods per sample		Ratio of brood size, island to mainland	Approximate distance offshore: kilometers
					island	mainland		
Agkistrodon piscivorus	Cedar Key	+	5.55	6.55	24	31	.85	11
Cnemidophorus lemniscatus and *arubensis*	Aruba	+	1.02	2.55	240	38	.40	50
Cnemidophorus tigris and *bacatus*	S Pedro Nolasco	+	1.85	2.04	48	30	.91	25
Cnemidophorus tigris and *martyris*	S Pedro Mártir	+	1.29	2.04	27	30	.63	50
Crocodylus acutus	Hispaniola	+	23.8	44.0	–	80	.54	550
Crotalus durissus and *unicolor*	Aruba	+	6.46	18.17	14	6	.36	30
Crotalus mitchelli	El Muerto	+	3.67	5.50	3	10	.67	10
Crotalus viridis	Los Coronados	+	2.57	8.67	7	12	.30	16
Elgaria multicarinata	Los Coronados	+	8.8	12.75	30	40	.69	16
Holbrookia propinqua	Padre	+	3.21	4.48	123	69	.72	3
Iguana iguana	Curaçao	+	17	35.5	23	11	.49	70
Mabuya caissara	São Sebastião	+	3.75	4.80	8	46	.78	2
Mabuya macrorhyncha	Vitoria	–	3.60	2.75	5	24	1.31	7
Mabuya macrorhyncha	Buizos	–	3.29	2.75	35	24	1.20	7
Mabuya macrorhyncha	Queimada Grande	+	2.28	2.75	46	24	.83	33
Sceloporus variabilis and *cozumelae*	Cozumel	+	1.8	3.2	12	10	.56	6

TABLE 6. Change in clutch and litter sizes from relatively aseasonal tropics (such as evergreen forest) to relatively seasonal climates (caatinga, deciduous forest, thorn scrub, temperate)

Species	Increase in more seasonal climate	Mean no. of eggs or young in clutch or litter		N = broods per sample		Ratio of brood size, seasonal to aseasonal	Estimated geographic scope of samples: hundreds of kilometers
		seasonal	aseasonal	seasonal	aseasonal		
Ameiva ameiva	+	5.6	3.6	80	15	1.5	22
Ameiva undulata	+	5.3	3.3	9	8	1.6	10
Basiliscus vittatus	+	6.3	3.9	11	40	1.6	20
Boa constrictor	–	17.8	30.3	6	6	.6	50
Bothrops atrox-asper	+	58	28	4	16	2.1	30
Cnemidophorus deppii	–	2.7	3.0	13	11	.9	16
Cnemidophorus lemniscatus	+	2.6	2.0	94	5	1.3	4
Coniophanes fissidens	+	3.1	2.6	8	36	1.2	25
Crotalus durissus	+	24	18	6	6	1.3	40
Dipsas catesbyi	+	3.1	2.1	9	19	1.5	30
Iguana iguana	–?	31	35	31	11	.9	6
Imantodes cenchoa	+	2.6	1.7	7	18	1.5	25
Leptodeira annulata	+	8.2	4.1	10	36	2.0	25
Mabuya mabouya	?	4.7	5.2	15	10	.9	20

tolerated in an active, vagile animal than in one that is cryptic, sluggish and sedentary.

One of the commonest correlations found by various authors is that of a small mean clutch in unfavorable years vs a large clutch in "good" years in the same area. Desert reptiles especially may have their egg production inhibited by scanty precipitation, as described by Mayhew (1965, 1966a, 1966b), Pianka (1970), Martin (1977) and Worthington (1982). These authors graphically described the effects of "dry" years upon the species they studied, but in other species such factors may have affected samples without being detected.

Length of growing season is obviously one of the important physical factors affecting demography; it is shortened from south to north and from low to high altitude, sometimes with profound effect on the species' ecology. Maturity in one or both sexes may be delayed, with lengthening of generation, and the number of clutches per growing season may be reduced. Combined, or even separately, these factors may so reduce the reproductive potential that a population can scarcely replace the losses occurring through normal mortality. As an evolutionary adjustment in partial compensation, clutch size may increase. This may be accomplished without unduly overburdening the gravid female by increasing adult size in the local population (without increasing egg size). Or it may be accomplished just as well by increasing only the adult female's size while the male is unchanged. In either case the female's egg capacity is increased.

Table 7 shows change in clutch and litter size in response to change in latitude in wide-ranging species for which available records represent a substantial north-south span. For each species the ratio of clutch-size of northern to southern samples was calculated. For some species having adequate records, two or more such ratios were calculated to show separately latitudinal changes in distinct climatic regions such as the West Coast, Great Basin, and Great Plains. Species that are primarily tropical were not included, nor were insular and high montane samples. In species for which many samples were available, they were pooled to produce composite means for comparison of northern and southern clutches. For instance, in *Uta stansburiana* mean clutches of 3.29 (Washington and N Oregon), 2.85 (SE Oregon), 3.75 (SW Idaho), 2.77 (NW Nevada), 4.09 (NW Utah) and 3.22 (NW Colorado) were combined for a composite northern sample averaging 3.33; those of 3.26 (S Nevada), 3.31 (Kern Co., California), 3.20 (Baja California), 4.12 (S Arizona), 3.3 (S New Mexico), and 3.9 (W Texas) were combined for a southern sample of 3.5; the composite means of 3.35 to 3.5 indicated a north-to-south ratio of .96 to 1.0, approximate parity.

Table 7 shows such latitudinal trends in clutch size in 47 cases in 45 species. In 62% there is northward increase. For all instances combined the average change is a northward increase of 19%. Within the sample the trends are notably different between turtles, lizards and snakes. In turtles 100% show northward increase of clutch, with an overall average increase of 75%. In snakes 60% of those tested show northward increase, with an overall average increase of 13%. In lizards 50% of those tested show northward increase, with an overall average increase of 1%. It should be noted that all but one of the turtle species investigated are aquatic, and their weightless state in a water medium doubtless renders it easier for them to increase their clutches without overburdening of the female. Snakes, habitually resting sprawled and prostrate on the ground surface, also have less serious problems with gravity in carrying their eggs than do quadrupedal (or bipedal) lizards. Probably for this reason, snakes have been found to have a consistently higher relative clutch mass than do lizards (Seigel and Fitch, 1984), and perhaps can increase clutch size with less stress than would be involved in a lizard.

Decrease in clutch and litter size from south to north occurred in 44% of the lizards tested in Table 7, 36% of the snakes but none of the turtles. It is necessary to explain why these species, departing from the trend found in the majority, decreased their litter size northward, despite the shorter growing season. However, in most instances at least, the southern populations that produce larger clutches than their northern counterparts also have larger body size. In such instances,

with egg size remaining the same, a larger clutch may result.

A trend of increased brood size at high altitude, paralleling the northward increase, is shown in Table 8, but this altitudinal increase in clutch seems to be much stronger and more consistent than latitudinal increase. Some increase with altitude occurred in each of the 22 cases tested, with an average gain of 28% in size of clutch. Seventeen of the cases tested were of lizards, only 4 were of snakes and none were turtles.

TABLE 7. Latitudinal trends in clutch size in wide-ranging species for which large samples are available

Species	Latitudinal Trend*	Mean Clutch		Ratio
		northern	*southern*	*northern/southern*
Chelydra serpentina	+ +	49	20	2.4
Chrysemys picta	+ +	10.3	5.8	1.8
Malaclemys terrapin	+	10.3	6.7	1.5
Pseudemys scripta	+	10.6	7.5	1.4
Terrapene carolina	+	4.2	2.7	1.6
Trionyx spiniferus	+ +	17.1	9.6	1.8
Cnemidophorus sexlineatus	−	3.1	3.3	.9
Cnemidophorus tigris	+ +	3.1	2.3	1.4
Crotaphytus collaris	=	6.7	6.7	1.0
Elgaria coerulea	+	4.7	4.2	1.1
Elgaria multicarinata	−	10.3	12.5	.9
Eumeces fasciatus	+	8.7	7.7	1.1
Eumeces obsoletus	+ +	15.2	10.8	1.4
Eumeces septentrionalis	−	8.8	11.7	.8
Gambelia wislizenii	+	6.3	5.6	1.1
Phrynosoma douglassi	− −	11.4	21.8	.5
Sceloporus graciosus	−	3.5	4.9	.7
Sceloporus occidentalis	+	10.3	9.2	1.1
Sceloporus magister	− −	6.3	9.7	.6
Sceloporus undulatus	+	9.5	7.1	1.3
Scincella lateralis	+	3.4	2.9	1.2
Uta stansburiana	−	3.3	3.5	.9
Agkistrodon contortrix	+ +	5.9	4.5	1.3
Agkistrodon piscivorus	+	7.7	6.6	1.4
Crotalus horridus	− −	8.5	12.6	.7
Crotalus ruber	+ +	8.7	3.3	2.6
Crotalus viridis	−	7.8	8.6	.9
Diadophis punctatus	−	4.4	5.2	.8
Heterodon platyrhinos	+	25.1	20.6	1.2
Lampropeltis getulus	+	10.6	9.8	1.1
Lampropeltis triangulum	+ +	8.4	5.4	1.6
Nerodia fasciata	+	20.4	18.4	1.1
Nerodia sipedon	+	22.6	18.0	1.3
Nerodia taxispilota	+	33.9	28.0	1.2
Opheodrys aestivus	+	5.7	5.4	1.1
Opheodrys vernalis	+	7.1	5.8	1.2
Pituophis melanoleucus	=	6.8	6.9	1.0
Regina septemvittata	−	9.3	12.2	.8
Sistrurus catenatus	+	8.2	5.9	1.4
Sistrurus miliarius	−	5.2	6.8	.8
Storeria dekayi	+	13.3	11.6	1.1
Storeria occipitomaculata	−	8.2	9.0	.9
Thamnophis elegans	− −	8.8	12.7	.7
Thamnophis sirtalis (eastern)	+	20.8	19.5	1.1
Thamnophis sirtalis (central)	−	16.4	19.1	.9
Thamnophis sirtalis (western)	−	12.2	13.9	.9
Virginia striatula	+	5.2	4.7	1.1

* + + northern increase strongly indicated; + northern increase weakly indicated; = no latitudinal change indicated; − southern increase weakly indicated; − − southern increase strongly indicated.

TABLE 8. Change in clutch and litter sizes with altitude

Species	Increase at higher altitude	Mean no. of eggs or young in clutch or litter		N = broods per sample		Ratio of brood sizes, high to low altitude	Estimated geographic scope of samples: hundreds of kilometers
		low alt.	high alt.	low alt.	high alt.		
Cnemidophorus inornatus	+	2.3	3.3	77	26	1.4	4
Cnemidophorus tigris	+	2.5	4.1	--	--	1.6	.5
Crotalus lepidus	+?	3.9	6.0	17	6	1.5	12
Crotalus pricei	+	5.3	6.3	12	7	1.2	11
Crotalus triseriatus	+	4.6	5.6	5	10	1.2	16
Elgaria coerulea[1]	+	4.5	5.5	14	10	1.2	2
Elgaria coerulea[2]	+	3.8	7.0	71	7	1.8	3
Elgaria coerulea[3]	+	4.6	5.2	40	54	1.1	3
Sceloporus aeneus	?	5.2	6.8	9	4	1.3	--
Sceloporus cyanogenys	?	13.4	17.7	9	25	1.3	--
Sceloporus graciosus	+	2.4	3.1	23	10	1.3	.1
Sceloporus jarrovi	+	7.1	8.4	154	106	1.2	.1
Sceloporus malachiticus	+	4.2	6.0	10	44	1.6	9
Sceloporus merriami	+?	3.7	4.5	27	>100	1.2	--
Sceloporus occidentalis[4]	+	8.2	8.8	17	24	1.1	1
Sceloporus occidentalis[5]	+	11.3	13.4	41	24	1.2	.1
Sceloporus occidentalis[6]	+	9.9	11.2	7	15	1.1	4
Sceloporus occidentalis[7]	+	8.2	10.3	27	?	1.3	2
Sceloporus occidentalis[8]	+	6.5	8.0	15	13	1.2	1
Sceloporus occidentalis[9]	+	7.2	8.7	43	41	1.2	< 1
Sceloporus occidentalis[10]	+	6.3	7.8	6	17	1.2	< 1
Thamnophis sirtalis	+	10.5	12.2	11	11	1.2	1

[1] SW Oregon
[2] NW California
[3] Central California
[4] SW Oregon
[5] Donner Pass, California
[6] Nevada
[7] Central California coast
[8] Kern County, California
[9] Los Angeles County, California
[10] San Diego County, California

Table 6 tests a group of tropical species, showing change in clutch or litter size from relatively aseasonal areas such as rain forest to areas having distinctly seasonal climates, usually characterized by pronounced dry seasons. There is strong tendency for brood size to increase from aseasonal to seasonal areas; 75% show some increase, and the average change is a 37% increase. Seeming exceptions to the trend may result from unreliably small samples in some. In other instances the animals in aseasonal habitats may be larger than their counterparts in harsher climates, and large body size is usually associated with high production of eggs or young.

Table 5 tests changes in clutch and litter sizes from 14 coastal islands to adjacent mainland areas in 13 kinds of reptiles. In 5 instances the insular populations have differentiated sufficiently to be considered specifically distinct from the mainland populations that they represent, in 3 other instances the insular populations are considered to be distinct subspecies, while the remaining 3 are not distinguished taxonomically. However, in 13 of 15 instances there is marked reduction in clutch from mainland to island, with average reduction of 30%. Dwarfing of the island populations was found to have occurred in most instances. The individual egg or neonate is relatively large in most instances; an extreme example is the egg of *Cnemidophorus martyris* (Walker, 1980).

Longitude as such cannot affect clutch size, but climatic changes notably from mesic to xeric, or *vice versa,* occurring along longitudinal gradients, may be important. Evidence of longitudinal change was found in 27 of the 137 species studied; 19 increase clutch or litter size from west to east while only 8 increase in the opposite direction. The commonest pattern found was in the snakes of the eastern United States; 11 undergo reduction of clutch or litter from the eastern or northeastern United States to the

western edge of the deciduous forests or to the Great Plains, namely *Agkistrodon contortrix, Carphophis amoenus, Coluber constrictor, Crotalus horridus, Diadophis punctatus, Elaphe obsoleta, Farancia abacura, Lampropeltis getulus, Lampropeltis triangulum, Micrurus fulvius* and *Thamnophis sirtalis.* Five species of snakes undergo increase in clutch or litter from the West Coast to the Great Plains or the Great Basin or inland valleys, while only 2 increase in the opposite direction. In the south-central United States 4 species of lizards increase their clutches from west to east, and 3 decrease. Of far western lizards, 3 increase their clutches inland and 2 increase them in coastal climates.

The majority of snake species which increase clutch size eastward in the United States also undergo an increase in body size to the eastward. It is not clear why this trend should be so prevalent, but perhaps it is linked with the availability of shelter, which is much better in the eastern forests than in more open country of the forest-grassland ecotone or the Great Plains farther west. In xeric-adapted lizards of the Southwest, there seems to be a tendency for the clutch to increase from a low level under the climatic rigors of the Mohave and Colorado deserts to a larger brood under the somewhat more mesic environments created by summer rainy seasons in regions to the eastward.

A few species such as *Cophosaurus texanus, Nerodia rhombifera, Nerodia sipedon, Pituophis melanoleucus,* and *Thamnophis sirtalis,* seem to have maximum clutch or litter size in one restricted portion of the range, and reductions in various directions from those centers. For nearly all species for which 4 or more geographic samples were available, the pattern was non-clinal and irregular.

Intraspecifically, body size of female and brood size are consistently correlated. Relatively large females tend to produce more eggs or more young, regardless of whether female size results from advanced age, unusually accelerated early growth in a favorable season, or inherent tendency in a local population. Many of the samples cited in the species accounts above may be biased in having females that average larger or smaller than the norm for their species, with their productivity affected accordingly. Timing of field work could affect results in some instances; at the beginning of the breeding season a high proportion of old and large adult females would be represented in an egg-bearing series, whereas later in the season a higher proportion of newly matured females with smaller clutches would be found.

Increased female bulk generally increases potential clutch size, and is hence subject to natural selection as part of a species' reproductive strategy. This strategy seems to apply in many species, for instance in *Sceloporus occidentalis* populations in the northern part of the range and at high altitudes where the growing season is short and the number of clutches is correspondingly reduced. Thus increased female size is in some instances part of a strategy for increased reproductive output, but in other instances it may have quite different significance. Body size is probably influenced by many interacting environmental and genetic factors which differ from species to species. In snakes, which must swallow their food entire, the sizes of the commonest potential prey species in different parts of the range must be the bases for intensive selection, causing local populations to differentiate.

Hatchlings and neonates also may have made evolutionary adjustments in their body size to exploit most effectively whatever kinds of prey are most available to them. Their food may consist of prey entirely different from that utilized by adults of the same species. For instance, adult watersnakes of the genus *Regina* prey chiefly on newly molted crayfish, whereas their neonates take dragon fly nymphs. Adult *Crotalus viridis* take ground squirrels, wood rats, gophers and immature rabbits, but their neonates depend on mice, lizards and spadefoot toads. Adult *Agkistrodon contortrix* take mainly rodents, but their neonates eat juvenile skinks and snakes, and small shrews. The size of the hatchling or neonate is, of course, closely correlated with the number in a brood.

In terms of reproductive effort *per individual offspring,* the 137 species studied vary over a wide range; *Diadophis puncta-*

tus, Scincella lateralis and *Uta stansburiana* are among those species that make relatively large investments, whereas the cheloniids, *Chelydra, Phrynosoma cornutum,* and *Nerodia* species represent the opposite extreme in making relatively small investment per offspring but producing large broods. Presumably there is some margin for intraspecific adaptational change in the size ratio of hatchling or neonate to parent. In *Coluber constrictor flaviventris,* egg weight averages 3.7% of female weight, whereas in the similar *C. mormon,* considered conspecific until recently, egg weight averages 11.4% of female weight (Fitch, Brown and Parker, 1981).

Increase in the relative size of the egg or neonate (e.g. *Coluber mormon* compared with *C. constrictor flaviventris*) must in most instances involve compensatory reduction in number of offspring in the brood. Many of the intraspecific differences in clutch and litter sizes noted here may have their bases in such biotic factors. For most of the wide-ranging species of reptiles here discussed, there are still few samples of clutch size available, and in most cases these are geographically remote.

For 64 of the 137 species studied, only two geographic samples apiece of clutch or litter size were available. Differences between such samples might naturally be assumed to represent trends such as increase from south to north or west to east. However, among the species represented by three samples, only 7 of 22 showed a consistent geographical trend. One tends to assume that in each species geographically intermediate populations still unsampled will be found intermediate in clutch size and will fall into clinal patterns. Actually most of the evidence is to the contrary. In many instances neighboring populations have been found to differ from each other about as much as relatively remote populations differ. Perhaps when much larger and more numerous samples have been accumulated, the patterns discerned will be found to consist of complex mosaics based upon highly localized environmental differences that overshadow broad trends, such as those of latitude.

From the foregoing observations it is evident that the factors controlling clutch and litter size are complex, and the data assembled here provide only a partial and imperfect understanding of them. However, several conclusions are definitely indicated. First, there is no universal trend of geographic variation, but each species differs from the others in the amount and direction of its variation. Second, the most consistent trend of variation found was that from mainland to insular populations, which showed reduction in clutch with increase in relative size of egg and hatchling (or neonate), and usually reduced adult size. Third, a fairly consistent trend was increase in clutch from low to high altitude. Fourth, species ranging from relatively aseasonal tropical areas into areas with severe dry seasons or cool seasons increase their clutch size in the more seasonal climates. Fifth, the majority of wide-ranging species (some 62% of those tested) show northward increase in clutch size. The trend is strongest in turtles, less developed in snakes, and weakest in lizards. In many instances there is associated increase in both body size and age at maturity. Ostensibly the increased clutch compensates in part for the fewer clutches in the shortened season of activity northward. Local shelter, food sources, and predators all provide potent selective forces which influence size of clutch or litter, but unlike climatic factors, do not produce clinal trends.

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APPENDIX I

Alphabetical list of species indicating records of clutches or litters obtained by the author and collaborators (boldface), and those obtained from examination of museum specimens: KU = Natural History Museum, University of Kansas; MVZ = Museum of Vertebrate Zoology, University of California; TU = Natural History Museum, University of Texas, AMNH = American Museum of Natural History, CU = University of Colorado Museum of Natural History.

Ameiva festiva KU Costa Rica 2, 3, 3, 3, 3, 4.
Ameiva undulata KU Yucatan 2, 4, 5, 5, 5, 6, 7, 7, 7; Nicaragua 1, 2, 4, 4, 5, 5; Costa Rica 2, 3.

Basiliscus vittatus KU, Campeche, Yucatan, Guerrero 3, 3, 4, 4, 4, 5, 5, 5, 5, 5.
Bothrops atrox AMNH, Peru 8, 15, 23.

Cnemidophorus deppii Costa Rica: **1, 2, 3, 3, 4;** KU: Mexico, Guerrero (2, 2), Oaxaca (2, 3, 3, 3); Nicaragua: (2, 3, 3, 4, 4, 4).
Cnemidophorus tigris Texas, Reeves Co., $\bar{x}$ = **2.12** in **16;** KU Sonora (2, 2, 2, 2, 3, 3, 3, 3), Sinaloa (2, 2, 2, 2, 2, 2).
Coluber mormon MVZ California, Alameda Co. (8, 9); Modoc Co. (3, 5, 5, 6, 6); Siskiyou Co. (4, 6); Shasta Co. (6, 6, 10); Sonoma Co. (4, 6, 6, 6, 7); Trinity Co. (2, 3, 3, 4, 9); Canada, British Columbia (4, 6, 6, 7, 8).
Crotalus horridus NE Kansas: **5, 5, 6, 8, 9, 10, 11, 11, 14; 8.5** (4-12) Shenandoah Natl. Park (W. H. Martin, III, pers. comm.); **9.3** ± 0.5(4-14) in 20.
Crotalus viridis Kansas: **5, 6, 7, 8, 8, 9, 10, 10, 11, 11, 11, 12, 18;** Ft. Hays St. Univ., Kansas 7, 9, 16; KU, Kansas 6.

Elaphe obsoleta NE Kansas $\bar{x}$ = **9.67** (5-14) in **6.**

Holbrookia maculata KU Arizona (4, 6, 6, 6, 7); Kansas $\bar{x}$ = 4.90 (2-9) in 61; Nebraska $\bar{x}$ = 4.08 (2-6) in 14; Mexico, Chihuahua $\bar{x}$ = 5.25 (3-9) in 13; MVZ, Arizona $\bar{x}$ = 6.75 (7-10) in 8; New Mexico (4, 6, 9); Mexico, Sonora $\bar{x}$ = 7.18 (4-9) in 11

Iguana iguana NWI, Curaçao, $\bar{x}$ = **17.0** ± 1.13 (10-30) in 23 (W. L. Backhuis, pers. comm.).

Lampropeltis calligaster KU Kansas (7, 9).
Leptodeira annulata KU, El Salvador and Nicaragua (6, 8, 8, 9, 10).

Mabuya mabouya KU, Panama (3, 4, 4, 5, 5).

Nerodia sipedon NE Kansas (**23, 34**); KU Kansas (7, 10, 10, 12, 12, 13, 15, 17, 21, 26).

Ophisaurus attenuatus NE Kansas **9.83** ± 1.19 (5-17) in **42.**

Pituophis melanoleucus NE Kansas (**9, 12, 13, 14, 16**) miscellaneous (**8, 8, 12, 5, 6, 7, 5; 9, 5, 6, 5, 9, 6, 4, 5, 4, 7; 4, 5, 4, 5, 5, 5, 5, 4, 5; 12, 13** (Charles E. Shaw, pers. comm.)

Sceloporus graciosus California, Kern Co., Greenhorn Mountains $\bar{x}$ = **6.3** (4-8) in **10;** Oregon, Jackson County, Union Creek $\bar{x}$ = **2.88** (2-4) in **16;** Josephine Co., Illinois River $\bar{x}$ = **2.72** (2-3) in **7;** MVZ, Washington, 2, 3, 3, 3, 5; Oregon, eastern counties, 3, 3, 3, 3, 3, 4, 4, 4, 4, Josephine Co. 3; Idaho (4); California, Siskiyou Co. (3), Modoc Co. (3, 4, 4, 5), Shasta Co. (4, 6), Riverside Co. (3, 3, 4, 4, 4, 5) San Bernardino Co. (3, 4, 4, 5); Nevada, Humboldt Co. $\bar{x}$ = 3.5 (2-5) in 10; Mexico, Baja California, $\bar{x}$ = 3.13 (1-5) in 7.
Sceloporus occidentalis California, Kern Co., Kern Canyon $\bar{x}$ = **6.50** in 8; Greenhorn Mountains $\bar{x}$ = **8.50** ± 0.32 (6-11) in 16; San Diego County, Cuyamaca Mountains $\bar{x}$ = **7.5** (4-10) in 10; Oregon, Jackson and Josephine cos., Rogue River Valley $\bar{x}$ = **8.19** (8-12) in **16;** Klamath County, Klamath River $\bar{x}$ = **9.25** (6-12) in **19;** MVZ California, Inyo Co. (7, 9, 14); San Bernardino Co. 7.00 ± 0.64 (3-11) in 14; San Diego Co. (5, 5, 8, 10, 11); Idaho, 8, 8, 9, 14; Oregon, Clackamas, Crook, Wheeler cos. 4, 6, 7, 7, 10, 11; Klamath Co. 5, 5, 8, 8, 8.
Sceloporus scalaris KU, Mexico, Michoacan $\bar{x}$ = **6.92** ± 0.43 (4-9) in 12.
Sceloporus undulatus Colorado, **8, 9, 10, 12, 12, 13, 14; 7, 7, 7, 8, 8, 9, 9, 10, 10, 10, 11, 11, 12, 12, 12, 13;** CU: 7, 8, 8, 9, 9, 9, 9, 9, 10, 10; 4, 7, 7, 8, 9, 9, 10, 11, 15.
Sistrurus catenatus NW Missouri $\bar{x}$ = **6.3** (5-10) in 17 (R. Seigel, pers. comm.).
Sphenomorphus cherriei KU Guatemala (2, 3, 3, 3).
Storeria dekayi NE Kansas $\bar{x}$ = **11.55** (5-20) in **9;** KU Kansas (6, 8, 9, 10, 13, 21).

Tantilla gracilis KU Kansas, 1, 1, 1, 1, 2, 2, 2, 2, 2, 2, 2, 3.
Thamnophis elegans Oregon **8, 8, 9, 10, 10, 10;** California **6, 8, 10, 10, 12, 14;** MVZ Idaho (9, 9, 9, 11, 12, 14); Canada, British Columbia (4, 10).
Thamnophis errans Mexico, **6, 7, 8, 10** (W. W. Tanner, pers. comm.).
Thamnophis ordinoides MVZ, Washington (4, 6, 7, 7, 8); Canada, British Columbia (4, 8, 9, 11).
Thamnophis proximus KU, Kansas (6, 10, 10, 11, 12, 13, 14, 22, 28); Texas (4, 10, 15).
Thamnophis sirtalis NE Kansas $\bar{x}$ = **19.15** (9-42) in **34;** SW Oregon and NW California, 11.32 ± 0.97 (5-23) in **22.**

Tropidoclonion lineatum KU, Kansas (3, 3, 6, 7, 11).

Urosaurus ornatus TU, Texas, Presidio Co. $\bar{x} = 6.27$ (5-10) in 22.

Uta stansburiana KU, California, Kern Co., lower Kern Canyon and adjacent San Joaquin Valley, $\bar{x} = 3.5$ (3-6) in 14; Walker Pass, 1530 m, $\bar{x} = 3.09$ (1-4) in 11; San Diego Co. above 900 m, $\bar{x} = 2.35$ (1-3) in 14; MVZ, California, Imperial Co., $x = 2.93$ (1-5) in 15; Riverside Co., $\bar{x} = 3.6$ (1-6) in 32; San Bernardino Co., $\bar{x} = 2.95$ (1-5) in 21; Idaho (2, 3, 4, 4); Oregon (1, 2, 3, 3); Nevada, Churchill and Lander cos. $\bar{x} = 2.86$ (2-4) in 7; Humboldt Co. $\bar{x} = 2.58$ (1-4) in 12; Lyon Co. (2, 2, 3); Washoe Co. (3, 3, 4, 4); Texas, Loving and Reeves cos. $\bar{x} = 3.1$ (2-4) in 10; New Mexico, Rio Grande Valley, $\bar{x} = 2.96$ (1-5) in 53; Washington (3, 4); Mexico, Baja California del Norte, $\bar{x} = 3.44$ (2-6) in 36.

APPENDIX II

Alphabetical list of species, and sources of information concerning their clutch- or litter-sizes. Publications listed in the Literature Cited are here abbreviated to the authors' initials and the year of publication. Following these are figures representing separate clutches or litters, or their means (in boldface), with ranges and standard errors of the means if these are known. Separate clutch counts are listed in sequence of increasing numbers, except that where different geographical areas are represented, series are segregated accordingly.

Agkistrodon contortrix PA 65: **5.6** (3-11) in 20; WBA 55: 5, 5; DAA 01: 6; AJB 48: 5, 9; CMB 23: 4, 6, 8; GEB 98: 7; HLB 29: 6; RWB 50: 3, 6; WLB & PWS 50: 5; CCC 58: 1, 4, 4, 4, 6; LC 49: **3.0** in 7; RFC 49: 5, 5, 6, 7, 7, 10, 10; WLC 48: 5, 8; RC 38: 6, 10, 10; ERD 15: 7; JSD 39: 5; HSF 60: **5.25** ±0.21 (2-13) in 88; HSF 70: **3.0** in 7; LCF 48: 5, 10, 12; EVG 53: 5, 6; RLH 45: 4; WGL 29: 7; RHM 45: 2, 5, 6, 7, 7, 8; CJM 61: 6; HM 54: 14; WTN 48: 11; GWS & SK 82: 4; AGS 40 and 45: **6.0** (3-10) in 19; PLS 52: 6; PWS 61: 3, 4, 5, 8, 11; RES 28: 8; AHW & AAW 57: 4, 5, 6, 7.

Agkistrodon piscivorus ERA & DS 48: **6.55** ±0.30 (3-12) in 31; CRB 81: **7.68** ±0.4 in 24; CCC 58: 4; RGW 70: 6; CWW 66: **5.55** ±0.31 (3-8) in 24; AHW and AAW 57: 2, 2, 2, 2, 3, 5, 6, 6, 7, 7, 7, 7, 9, 9, 9, 10, 12, 12, 15.

Alligator mississippiensis DCD & TCH 80: **37.5** ±1.35 in 67; MJF 74: **33.1;** THG & WRM 78: **30.3** ±2.58 in 14; TJ 69: **38.9** (2-58) in 315; WDM 77: **30** (12-44) in 55.

Ameiva ameiva WED 78: **3.72** (2-6) in 13; LJV 82: **5.6** (1-9) in 80.

Ameiva festiva RES 68: **2.2** in 87.

Arizona elegans RDA 79: **8.4** ±0.7 in 7; LMK 46: 9, 12; 10; 4, 5, 6, 7, 9; 23; 4, 10; 3, 7.

Basiliscus basiliscus RWV 82: **10.4** (6-18) in 38; **8.4** (3-13) in 34.

Basiliscus vittatus MA 60: 16; RC & AD 40: 14; HSF 73: **3.17** ±0.20 (2-4) in 12; 3, 5, 6; **4.1** in 9; HH 63a: **4.2** in 25; HMS & LEL 45: 7; JEW 51: 16.

Boa constrictor JRD & PS 77: 6, 20, 24, 28; HSF 70: 11, 12, 15, 16; LMH & RWM 69: 17, 36; RRM 24: 63; RRM & FWU 94: 41.

Bothrops atrox WB 46: 8, 9, 11, 16, 38; JRD & PS 77: 17, 22; WED 78: 18, 24; HH 64: 48-86; 28, 57; 64, 65, 71; RMH 24: 29, 30, 32, 56, 56; JS & HFH 65: 32.

Caiman crocodilus JRD & PS 77: 25, 30, 33; JL 80: **33.0** (23-41) in 37; FM 81: **22.81** ±1.53 (19-31) in 17; MS & JRD 77: **29.02** (17-38) in 200.

Callisaurus draconoides ERP & WSP 72: **4.42** in 73; WWT & JEK 75: **4.53** in 14; LJV 77: **4.5** (3-7) in 12; LJV & RDO 77a: **4.6** (1-8) in 34.

Caretta caretta JBA & LWA 81: **117** ±4.31 in 393; DKC 82: **126** in ?; NBF & JIR 84: **120** in 1897; CRL & RWB 71: **110** (44-172) in 46; RK 75: **107** (58-163) in 185.

Carphophis amoenus and *vermis* RWB 60: **2.64** ±0.23 (1-4) in 14; FMB 59: **3.2** in 7; DRC 70: **2.87** (1-5) in 118; AHW & AAW 57: 2, 2, 2, 3, 3, 4, 5, 8, 8.

Chelonia mydas KAB 80: **112.3** in 2040; LME 80: **129.6** (91-158) in 27; HH 71: **104.7** (83-184); **110** (50-200); **110** (18-193), **115.5** (53-181), **142** (87-226), **87** (67-107) in 10.

Chelydra serpentina DAH 69: **49** (31-87) in 102; JBI 77: **16.6** ±1.6 (14-20) in 8; DJL & MEO 77: **33.9** ±10.03 (18-66) in 46; PJP & MMA 80: **30.9** ±2.80 (16-59) in 16; RCV 81: **44** (?-85) in 70; JBW & GWM 73: **19.9** (12-42) in 20; CLY 79: **46.02** in 53.

Chrysemys picta FRC 54: **6.3** (3-8) in 48; **4.7** (2-7) in 12; **4.3** (3-6) in 13; JLC & EOM 73: **9.6** (1-22) in 28; **8.8** (2-15) in 46; JDC & DWT 82: **7.6** ±0.16 (2-11) in 129; LCF 48: **5.85** in 7; DJG 70: **11.9** in 10; JWG 68: **6.5** in 41; JML 54: **8.8** (5-11) in 13; IYM 68: **10** (5-16) in 101; RDM & DMS 83: **19.8** (17-23) in ?; EOM 73: **10.7** (3-16) in 22; **8.7** (6-14) in 49; **4.8** (2-9) in 15; **4.1** (1-6) in 41; **4.8** in 29; **8.8** in 10; CBP 67: **8.5** (5-11) in 26; JKT 78: **8.2** in 33.

Cnemidophorus arubensis JJS 83: **1.02** in 38.

Cnemidophorus bacatus JMW 80: **1.85** (1-3) in 48.

Cnemidophorus communis JMW 82: **6.6** in 7.

Cnemidophorus deppii WBD & HMS 53: 2, 2, 4, 4, 4; JPK 68: 2, 2.

Cnemidophorus gularis REB & GDS 72: **4.5** in 154; JJS 78: **3.13** (1-5) in 23.
Cnemidophorus inornatus JLC 71: **2.29** in 68; PAM 67: **2.15** in 16; TPS 83: **3.3** (2-5) in 26; **2.37** in 87; JMW 81: **2.23** (1-3) in 17; **2.07** (1-4) in 13.
Cnemidophorus lemniscatus WB 45: 2, 2, 2, 2, 2; JRL & LJC 73: **2.55** (2-5) in 94.
Cnemidophorus lineatissimus JMW 70: **4.78.**
Cnemidophorus martyris JMW 80: **1.29** ±0.09 (1-2) in 27.
Cnemidophorus ocellifer LJV 83: **2.67** (1-5) in 58.
Cnemidophorus parvisocius JMW 81: **1.75** in 40; **1.80** in 45.
Cnemodophorus sexlineatus EEB 56: **2.97** ±0.83 (1-5) in 67; CCC 60: **2.46** (1-6) in 82; DRC 76: **3.38** ±0.14 (3-4) in 8; HSF 58: **2.77** in 29; GAH 66: **3.1** ±0.30 in 32; JML 58: 5; SET 83: **3.4** (1-6) in 37; **3.38** (1-6) in 98; **3.70** (1-8) in 34; **3.53** (1-5) in 19; RJW 72: **2.8** in 15.
Cnemidophorus tigris GMB & JMW 73: **2.65** ±0.11 in 52; SRG 76: **4.1** in 56; LMH & RWM 69: 2, 2; CJM & GAH 66: **3.4** in 52; **2.2** in 117; PAM 67: **2.0** (1-3) in 5; ERP 70: **3.0** in 12; **2.56** in 9, **2.32** in 22; **2.37** in 46; **2.86** in 14; **2.44** in 18; **2.67** in 39; **3.09** in 12; **2.93** in 29; WSP 72: **2.05** in 45; WSP 73b: **4.0** ± 0.42 (2-6) in 8; **2.03** ±0.12 (1-4) in 25; JJS 78: **2.02** ±0.11 (1-4) in 43; LJV & RDO 77b: **2.9** (1-5) in 15.
Coluber constrictor PA 65: **9** (7-22) in 10, 7; WA 49: 10; CSB 03: 13, 21; RB 50: 22; FRC 42: 20, 21; CCC 58: 11; RC 42: 7, 14; RC & AD 40: 15, 20; RLD 07: 8; HSF 63a: **11.40** in 68; ERF 30: 8, 9, 9; EVG 53: 10; JBI 78a: 11, 12, 22; EAL 49: 19; RHM 45: 7, 12, 14, 16, 19, 20, 31; DAR 60: 19; DWT 59: 6, 15; OCV 31: 16; JEW 70: 18, 18, 27; JEW & JM 51: 8; AHW & SCB 15: 5, 9, 11, 14; AHW & AAW 57: 25.
Coluber mormon JDC 59: 4, 4, 5, 5, 5, 8, 9, 13; HSF, WSB & WSP 81: **6.44** ±0.26 (4-11) in 43; RMS & RAP 49: 3; RLV, JM & PLR 62: 6; AHW & AAW 57: 4, 4, 6.
Coniophanes fissidens GRZ, SBH & SS 79: **2.53** ±0.19 (1-5) in 34; **3.20** ±0.61 (1-7) in 10.
Cophosaurus texanus REB, EDT & DWT 72: **6.1** ±0.03 in 244; AH 73: **2.8** (2-4) in 16; JMH 84: **3.1** in 25; CJ 60: **5.0** in 269; WSP 73b: **4.0** (3-6) in 3; LJV 77: **4.6** (3-7) in 12.
Crocodylus acutus SJI, JAO, CS & DGR 80: **23.8** in 80; FM 81: **44** (19-81).
Crotalus atrox BLA & JBM 79: **14.3** (6-25) in 9; LMK 56: **9.0** ±0.66 in 33; DWT 62: **9.9** ±0.69 (6-13) in 10; **12.7** ±0.5 (6-18) in 34; **16.1** ±0.4 (13-19) in 18.
Crotalus cerastes LMK 56: **10.8** ±0.97 (7-18) in 10; **8.96** ±0.53 (5-16) in 28.
Crotalus durissus BLA & JBM 79: 10, 21; LMK 56: 12, 18, 37, 47; 10, 12, 16, 19; PEV, AMMR & LJV 80: 21, 31.
Crotalus horridus JTC 82: 6; JWG 72: **12.6** ±0.5 (10-16) in 16; KDK 78: **8.4** ±0.37 (3-11) in 25; LMK 56: **9.71** in 7; **10.5** in 44.
Crotalus lepidus BLA & JBM 79: 3, 4, 5; 4, 6, 11; LMK 56: 3, 4, 8; 2, 2, 2, 3, 3, 3, 3, 4, 4, 5, 5, 5, 5, 8.
Crotalus mitchelli BLA & JBM 79: 2, 3, 4, 4, 5; 1, 3, 7; LMK 56: **8.66** ±0.67 (6-10) in 6; **5.50** ±0.43 (4-8) in 10; **3.33** ±0.56 (1-5) in 6.
Crotalus pricei BLA & JBM 79: 3, 4, 4, 4, 6, 8; 6, 6, 6, 8, 9; 4, 5; LMK 56: 4, 5, 6, 6, 7, 7.
Crotalus ruber LMK 56: **8.68** ±0.73 (3-20) in 28; **5.67** ±0.73 (3-12) in 15.
Crotalus unicolor GC, KHP & RMH 82b: **4.6** (3-8) in 9; 6, 7, 9, 9, 10, 14.
Crotalus vegrandis GC, KHP & RMH 82a: **4.2** ±0.5 (2-5) in 16.
Crotalus viridis RDA 79: **9.5** ±0.6 (5-14) in 23; JDC 59: 2, 5, 6, 9; JTC 82: 14, 14; LVD & RLW 84: **5.5** ±0.13 in 117; HSF 49: **8.3** (2-14) in 17; VPJG & DMS 84: **9.74** in 53; HRG 51: **5.50** (2-9) in 490; LMK 56: **6.58** (1-14) in 79; **7.84** (2-13) in 38; **8.67** (1-14) in 12; **11.43** in 308 [**11.86** in 149, part of preceding series]; **8.00** (6-13) in 5; **2.6** (1-4) in 7; AMW & RMH 50: **7.5** in 6.
Crotaphytus bicinctores WGR & WWT 62: **5.0** (3-8) in 6; **3.9** (2-5) in 7.
Crotaphytus collaris TGH 77: **7.2** in 88; LM 84: **6.9** in 86; **6.1** in 36; **6.6** ±0.2 in 25; WSP 73: **5.3** in 11; SET 78: **6.5** (3-11) in 74; LJV 77: **5.6** (4-7) in 5.

Dermochelys coriacea AFC & LO 59: **97** (73-145, 31.5 abnormal) in 6; JF 80: **114.52** in 27 (including 30.2 infertile); **144.74** (including 30.22 infertile); JRH 62: **88.06** (including many abnormal) in 95; **106** ±22 (including 30 abnormal); JVM 83: **63** (13-96) in 27.
Diadophis punctatus RWB 50: **3.77** ±0.32 in 13; FNB 59: 3, 3; FNB, MRG & FCB 79: **3.5** (1-7) in 202; HSF 75: **3.89** ±0.08 (2-10) in 300; JBI 78: 5, 6; CWM 65: **5.2** (2-10) in 20; HWP 56: 6; AHW & AAW 57: **6.45** ±1.00 (1-10) in 11.
Dipsas catesbyi GRZ, SBH & SS 78: **2.1** ±0.2 (1-4) in 20; **3.1** ±0.3 (2-4) in 9.

Elaphe guttata HBB & EB 58 & 62: 3, 5, 6, 7, 8, 8, 11, 13, 17, 21; HC 53: 4, 5; RSF 62: 13, 19; FG 68: **15.33** ±1.32 (8-30) in 20; JBI 78: 7, 8, 16, 28; JAM 57: 11; MVP 48: 18; JEW 51: 15.
Elaphe obsoleta PA 65: 7, 19; DAB & OAH 34: 16; FMB 59: 10; CCC 58: 9; FRG & BBC 59: 9; FG 69: 14, 14, 15, 17, 19; HKG 28: 9, 11, 14; JHH 11: 22; RMJ 50: 8; AHW & AAW 57: **14.4** in 20; **14.1** in 14.
Elgaria coerulea HSF 35: **5.50** (2-8) in 10; **7.00** (6-9) in 7; THL 46: 5, 5, 6, 7; RAP 59: **4.5** ±0.25 (2-6) in 14; JRS 79: **3.8** ±0.2 (2-7) in 71; **4.6** ±0.2 (3-9) in 40; **5.2** ±0.2 (3-9) in 54; LJV 74: **4.6** (3-8) in 16.
Elgaria multicarinata BRB 65: **13** (5-41) in 25; **10** (1-18) in 12; EDB, RAN & RMS 69: 14, 14; JDC 58: **7** in 3; **8** (3-17) in 18; HSF 35: **12.4** (8-15) in 7; HSF 70: **9.0** (8-11) in 9; **11.62** (6-17) in 13; **11.83** (5-20) in 13; SRG 72: **12.0** (9-17) in 9; CES 52: 12, 20.
Emydoidea blandingii ARC 37: "6-10"; JDC, DWT, GLB & RCV 83: **10.0** (3-15) in 90; PJP 84: **12.2** (8-18) in 50.
Eretmochelys imbricata AFC, HH & LO 66: **161.10** (53-206) in 57; PCMP 69: **158.14** ±4.72 (139-176) in 7.

Eumeces fasciatus FMB 59: **9.2** in 5; FRC 40: **9.15** in 26; RC 51: 6, 6, 8, 8, 9, 11, 13, 14; WEC, LJV, LDV & JWG 83: 6; HSF 67: **9.16** (4-15) in 64; JDG 82: 6, 6, 7, 8, 11; AER 58: **7.36** ±0.54 (5-12) in 11; EHT 35: 9, 10; RGW 70: 6, 7, 9, 9.

Eumeces obsoletus RJH & HSF 72: **12.3** ±0.53 in 37; MPS 78: **15.15** ±1.56 (8-32); **10.9** ±0.80 (5-20) in 132.

Eumeces septentrionalis WJB 43: **8.78** ±0.55 (5-13) in 19; RFC 55: 6, 7, 9, 10; FRG & BBC 59: 11, 18; JBI 75: 12, 13, 14, 15, 16; MS & RW 59: 9.

Eumeces skiltonianus FP 82: **4.7** in 6; RCS 54: 8 to 9 in 8; WWT 43 & 57: **4.21** ±0.19 (2-6) in 19; JV 22: 5.

Farancia abacura WED & AS 58: 35; DWT 59: 27; AHW & AAW 57: **50.1** (25-104) in 7; **27.6** (11-50) in 10.

Gambelia wislizenii CLC 16: 1; HSF 70: 5, 5, 6; CJM 67: **7.3** in 10; WSP & ERP 76: **3.4** in 7; **5.9** in 52; **3.5** in 15; WGR & WWT 62: **4.81** in 11; **5.25** in 7; CES 54: 5; WWT & JEK 74: **6.5** in 19; KT 82: **5.6** in 15; **6.2** in 9; LJV 77: 5, 6.

Gopherus polyphemus JBI 80: **5.2** (1-9) in 32; JLL, JAG & WAM 80: **7.0** ±1.7 (4-12) in 47; **5.0** (4-7) in 9.

Graptemys ouachitensis JTC 82: 5, 12; RCV 80: **10.5** in 65; RGW 62: 3, 4, 5, 6, 7, 10.

Heterodon nasicus PA 65: 16; WJB 42b: 11; JCM 44: 7, 11, 13, 14, 17, 33; JEM 53: 11; JEM & GBR 52: 7; DFM 49: 11; DRP 69: **7.3** (4-16) in 14; 12; RCS 54: 5, 7, 9; MS 60: 5; MS & RW 59: 2.

Heterodon platyrhinos DRP 69: **25.1** in 20; **20.6** in 35.

Holbrookia maculata FRG & BBC 59: 3, 3, 5, 6; ALG 74: **7.00** ±0.34 in 21; DLD, SMJ & REB 82: **3.55** ±0.37 (1-7) in 38; WSP 73b: 9; LJV 77: **10.8** (8-12) in 5; RJW 72: **5.9** in 11.

Holbrookia propinqua FWJ & RKR 78: **4.48** (3-7) in 69; **3.21** (2-4) in 123.

Iguana iguana HSF & RWH 77: **30.5** ±2.10 (11-54) in 31; HH 63b: **35.45** ±1.67 (24-45) in 11; ASR 84: **40.6** (9-71) in 30.

Imantodes cenchoa GRZ, SBH & SS 79: **2.57** ±0.30 (1-3) in 7; **1.73** ±0.15 (1-3) in 18.

Kinosternon flavescens JLC & AED 72: **3.6** (1-6) in 29; JBI 75: **5.8** (4-7) in 13; JBI 84: **4.5** in 80; IYM & JK 72: **5.0** (4-5) in 21; RCV, JLB & CJM 82: **5.6** in 10.

Kinosternon hirtipes JBI 81: **2.87** (2-5) in 30; **4.37** ±0.24 (1-6) in 19; **4.12** ±0.41 (1-9) in 17.

Kinosternon subrubrum FSB 48: 2, 2, 2, 2, 2, 2; JWG 82: **3.1** in 168; JWG, JLG & JPS 80: **3.00** (2-4) in 23; JBI 79b: **3.08** ±1.30 in 26; **2.1** (1-3) in 12; **3.46** (2.5) in 13; IYM & JK 72: **5.0** (4-5) in 23; JTN 47: 4, 6.

Lampropeltis calligaster PA 42: 6, 11, 12, 13; CCC 58: 14, 14; RFC 54: 9; SED 60: 17; HSF 78a: **9.57** in 11; HKG 29: 6; EVG 53: 8; SCM 44: 11; RS 57: 8, 11; PWS 61: 9, 9; BWT & GC 80: 5, 13.

Lampropeltis getulus PA 65: 14; DAB & OAH 34: 14; CSB 03: 10, 17; CCC 58: 16; RC 34: 9, 10; RC & AD 40: 11; JTC 82: 11; EF 30: 8; HKG 28: 10; EVG 53: 5; JBI 78: 6, 17; JCK 51: 7; RHM 45: 10, 12; GHP 43: 7; PWS 61: 9, 9, 13, 13; JEW 51: 9, 12; AHW & AAW 57: 6, 7, 9, 9, 9, 16; RGZ 80: **4.92** (2-9) in 48.

Lampropeltis triangulum JTC 82: 7; SD 77: **8.9** (5-11) in 9; HSF & RRF 70: **6.7** ±0.46 (5-9) in 10; BWT & JBM 82: **5.5** (3-7) in 6; **5.25** ±0.42 (4-7) in 8; **5.50** ±0.66 (4-12) in 8; **5.44** ±0.35 (3-9) in 25; AHW & AAW 57: **12.78** (6-24) in 27.

Leptodeira annulata WED 78: 3; 6; HSF 70: **4.0** (2-7) in 34; TPH 40: 6, 7, 9; RLL & RSP 53: 10; EHT 49: 9.

Mabuya caissara PEV & RR-S 76: **5.06** (2-8) in 17; **4.58** (3-9) in 17; **3.75** (2-6) in 8; **4.75** (2-5) in 12.

Mabuya heathi DGB, LJV & CJB 84: **5.0** ±0.1 (2-9) in 131.

Mabuya mabouya MA 60: 4-7; WBD & JRD 61: 2, 3, 4; WED 78: **5.2** (4-6) in 10; HSF 70: 1, 2, 2; RGW 58: 3, 5; 4-6 in 10.

Mabuya macrorhyncha PEV & RR-S 76: **2.45** (2-5) in 11; **3.16** (1-6) in 12; **3.60** (2-4) in 5; **2.29** (2-4) in 35; **3.33** (2-3) in 3; **2.28** (2-4) in 46.

Malaclemys terrapin TAB & KLW 72: **8.5** ±0.7 in 11; WAM & JB 75: **9.8** ±2.6 (4-18) in 40; RP 73: **12.6** ±1.2 (8-17) in 9; RAS 80: **7.5** ±2.1 in 14.

Micrurus fulvius DRJ & RF 81: 3, 5, 6, 7, 7, 7, 8, 11, 13; HRQ 79: 3, 4, 5, 6, 7, 7, 9.

Nerodia erythrogaster PA 65: 8, 11, 13, 14, 22, 22, 22; 13, 16; AJB 48: 17; CCC 58: 17; RC 51: 8, 8, 10; RC & AD 40: 20; RAD 57: **12.0** (5-21) in 5; EVG 53: 5, 18; JHH 11: 13; CPK 79b: 4, 6, 9, 16, 22; WWM, JSM & HM 50: 15; PWS 61: 28.

Nerodia fasciata PA 65: 7, 13, 19; ERA 41: 3, 11, 41; MJA 32: 23; RFC 49: 12, 13, 14, 15, 18, 18, 22, 25, 27, 30, 35, 37; RC & AD 40: 25; LC 49: 13; WED & AS 58: 21; 10, 17, 32; JHH 11: 23; JPK 64: 12, 30; CPK 79b: 12, 16, 18; GPM 34: 17; DMO 78: **20.16** in 63; MS & RW 59: 12, 20; RDS & JWG 82: **21** (2-50) in 34; DWT 59: **16.4** (10-27) in 11; JEW 51: 10; AHW & AAW 57: 5, 14, 15, 23.

Nerodia rhombifera PA 65: 30; AJB 48: 14; TWB 63: **37.1** ±1.87 (27-56) in 20; FRC 37a: **27.13** in 18; CCC 58: 17; LC 49: 14; ERF 30: 43; HKG 28: 25, 34; EVG 53: 62; CPK 79: 16, 20, 22, 49; PWS 61: 23, 32; AHW & AAW 57: 36.

Nerodia sipedon RDA 82: **19.94** (9-41) in 31; PA 65: 10, 16, 16, 19, 23, 29; 11, 23, 35; MAB & DEM 77: **29.88** ±1.54 (15-66) in 55; FRC 42a: 16, 30, 44, 48, 49; JHC & PRE 58: **20.8** (6-34) in 14; RC 51: 8, 11, 19, 22, 22, 26, 27, 28; PEF 77: **11.8;** HKG 28: 36; EVG 53: 22; DAL 47: 24; THL 25: 15, 16, 18, 21, 23, 23, 28, 30, 45; RBL 48: 35; RHM 45: 11, 14, 14, 16, 17, 17, 19, 19, 19, 20, 21, 23, 31, 38; MS & RW 59: 12, 20; PWS 61: 8, 9, 11, 12, 17, 51; 13; 13,

32, 50; AHW & AAW 57: 7, 11, 13, 19, 23, 25.
Nerodia taxispilota RDS & JWG 82: **28** (7-63) in 51; DRW, JCM & WSW 82: **33.9** ±12.1 (19-63) in 23.

Opheodrys aestivus PA 65: 4, 6; CSB 03: 4; FMB 59: 4, 5; CCC 58: 3, 6,7; JTC 82: 10; RC 51: 4, 5, 7; RC & AD 40: 9; RFC 49: 5; LC 49: 6; SKG 84: **5.5** (3-7) in 10; EVG 53: 8, 10; JPK 64: 3; MVP 84: **6.1** ±0.21 (3-10) in 77; WMP & ALB 76: **5.27** ±0.45 (4-8) in 11; MS & RW 59: 12; PWS 61: 6; DWT 60: **4.7** (4-10) in 30; RGW 70: 5, 5, 8; WAW & KC 39: 5; AHW & AAW 57: 4.
Opheodrys vernalis PA 65: 5; FNB 33: **6.7** ±0.24 in 53; FRC 64: 7, 8, 8, 9; THF 68: 18, 18; DMG & FMC 80: **7.33** ±0.43 (4-10) in 15; PTG 75: 5, 5, 5; DWL 59: 2; HMS 63: 4, 8; WTS 54: **5.8** ±0.39 (5-15) in 25; AHW & AAW 57: 4.
Ophisaurus attenuatus APB 61: 11; ERF 30: 15; RHM 75: 5, 10; SET 84: **12.1** (7-16) in 7.

Phrynosoma cornutum REB 74: **20.25** in 12; **28.89** in 9; **25.73** in 11; **22.78** in 9; **29.04** in 8; **19.85** in 13; **29.83** in 6; **25.92** in 24; **32.92** in 12; CWH 74: **29.7** ±3.80 (13-45) in 21; WSP 73c: 25; LJV 77: **35.8** (25-47) in 4.
Phrynosoma douglassi JD 49b: 18; FRG 65: 6, 8, 10, 11, 11, 15, 21; SRG 71b: **16.7** (9-30) in 11; CWH 74: **22.8** ±3.71 (13-34) in 5; **23.5** ±1.88 (9-48) in 32; HJP 18: 10, 11, 14; RAP 51: 7; CFS 41: 15; VMT 42: 8; WWT 53: 7; WWT 54: 13, 13; WHW 53: 30.
Phrynosoma platyrhinos CWH 74: **5.6** ±0.33 (2-10) in 37; ERP & WSP 75: **8.4** in 46; WWT & JEK 73b: **6.66** (3-9) in 24; LJV 77: **7.8** in 6.
Pituophis melanoleucus PA 65: 18; EDB, RAN & RMS 69: 3, 6, 8, 9; CCC 58: 8; JTC 82: 9; RC & AD 40: 7, 9; RBC 35: 7; HKG 28: 12, 16, 18; RHI 45: **12.8** (5-23) in 22; JBI 75: 7, 16; JBI 78b: 5; LMK 47: **6.8** (3-12) in 13; 10; 8, 9, 12; 8, 9, 18; 4, 10, 11; DSL 67: 6; JMM 52: 9; WTN 51: 4, 5, 8; JGN 53: 10; CBP 43: 6, 6, 7; WSP & WSB 80: **8.37** (4-15) in 19; JV 22: 19; GCW 54: 13, 19; AHW & AAW 57: 7, 9, 10, 10, 10.
Podocnemis expansa CJRA & LFMP 82: **93.1** in 5582; JAR 64: **84** in ?
Pseudemys scripta FRC 37b: **10.5** (5-22) in 47; FRC 50: **7.0** (2-19) in 129; **9.3** (4-18) in 102; **7.6** ±0.24 (4-11) in 59; **9.2** in 67; JWG 82: **6.1** ±0.20 (2-15) in 73; **10.2** ±0.40 (6-17) in 48; JBI 77: 4, 4, 8, 8, 9, 9, 9, 9; GMT 82: **12.54** ±0.90 in 52; **11.09** ±0.77 in 68; RGW 61: **8.8** (1-12) in 6.

Regina grahami PA 65: 14; RJH 69: **18.6** (9-39) in 16; CPK 79b: 8, 10; CPK & JRD 80: 16; JPK 64: 6; RNM 59: 25; PWS 61: 9; RGW 70: 19; AHW & AAW 57: 6, 8, 10, 10, 13, 14.
Regina septemvittata DAA 01: 6, 12; BAB & ECB 74: **12.8** (8-17) in 10; CSB 03: 13; RC 51: 10, 11; WTN 51: 13; PWS 61: 7, 9, 12; AHW & AAW 57: 6, 8, 8, 9, 10, 10, 11, 12, 14, 13 (in 2 broods).

Sauromalus hispidus TJC 82: 21, 22, 24, 29.
Sauromalus obesus KHB 74: **7.8** (6-13) in 22; AAP 77: **8.0** (6-10) in 7 ?.
Sauromalus varius TJC 82: 16, 18, 23, 28, 32.
Sceloporus aeneus HSF 78b: **5.22** ±0.43 in 9; **6.75** in 4.
Sceloporus clarki HSF 70: 4, 7, 10, 10, 10; 22, 24; AH 73: **14.1** (9-19) in 9; RCS 54: **11** in 4; LJV 77: 19, 23; RGW 84: 7.
Sceloporus cyanogenys TC 64: **17.68** in 25; DH 59: **13.44** (6-18) in 9; JPK 60: 11, 17.
Sceloporus graciosus GMB & WWT 74: **6.03** (2-10) in 143; CLD 66: 4, 6; FRG 65: 3, 4, 4, 4, 4; SRG 75: **4.07** in 78; JGG, JED & JML 30: 3, 3; EWJ 74: **4.9** in 78; RMS & RAP 49: 7; FP 82: **8.4** in 12; SBR 77: **4.1** in ?; RCS & HBR 46: **3.33** (2-5) in 10; DWT 73: **3.8** in 72.
Sceloporus grammicus LJG & GC 80: **5.2** ±0.25 (3-7) in 39; AO & RB 84: **6.17** ±1.65 (3-9) in 46; JEW 51: **5.7** ±0.44 in 7.
Sceloporus jarrovi REB 79: **8.4** (3-16) in 106; **7.07** (2-15) in 154; WBD & HMS 53: **5.00** in 8; SRG 71a: **6.77** (2-12) in 85; DWT & NFH 73: **6.75** ±0.32 (2-11) in 52.
Sceloporus magister WSP & ERP 73: **8.4** in 14; CES 52: 7, 11, 11, 18; WWT & JEK 73a: 4, 5, 7, 7, 7, 10; DWT 76: **6.2** (2-9) in 22; LJV & RDO 74: **12.3** (10-18) in 4.
Sceloporus malachiticus KRM & OJS 71: **6.0** in 44; HSF 78b: **4.20** ±0.34 (3-6) in 10.
Sceloporus merriami AHC & REG 54: **3.74** ±0.14 (2-5) in 27; AED 81: **4.51** ±0.03 (3-7) in >100.
Sceloporus occidentalis JD 67: **8.15** in 27; SRG 74: **7.23** in 43; **8.7** in 41; EWJ & AA 76: **11.3** ±0.41 in 48; **13.4** ±0.57 in 24; JML 40: 7, 10; SBR 77: **10.3;** JJS 83: **10.35** (5-14) in 153; CES 52: 7, 13; RCS 54: 5, 12; RMS & RAP 49: 8, 8, 10, 11, 13, 13; WWT & JMH 72: **11.2** (7-15) in 15; JV 22: 7, 10; LJV 77: 7, 8.
Sceloporus poinsetti REB 73: **10.45** ±1.01 (5-23) in 40; REB 78: **10.75** ±0.58 (4-15) in 34; FP 82: **13.6** in 7; RCS 54: 7, 10, 10.
Sceloporus scalaris REB & JDC 81: **8.52** ±0.22 (3-14) in 153.
Sceloporus undulatus JA 81: **10.0;** FMB 59: **8.4** in 18; REB, DID & SMJ 81: **5.55** ±0.21 in 63; RWB 50: 10; FRC 42: 8; CCC 60: **9.0** (4-13) in 13; **7.6** (5-12) in 10; **6.23** (3-8) in 13; **9.00** (4-13) in 6; RC 51: 6, 8, 8; JWC 55: **7.6** (6-10) in 11; JD 49a: 8; CLD 66: 8; GWF, CHB & HPW 80: **7.00** ±0.48 in 23; JWF 76: **9.4** (8-12) in 11; JPK ms: **5.85;** GMF & KRM 77: **8.3** in 61; CMM 76: **8.0** in ?; CES 52: 8; PWS 61: 8; RCS 54: 8; CAT 55: 11; DWT & REB 72: **6.9** in 13; **9.3** in 18; **11.8** in 5; **7.8** in 8; RJW 72: **8.1** in 9; RGW 70: 8; MBV 75: **9.9** ±0.42 in 39; **7.2** ±0.26 in 29; LJV 77: **7.5** in 10; 10, 10.
Sceloporus woodi JFJ & SRT 74: **4.25** (2-8) in 162.
Scincella lateralis FMB 59: **3.9** in 10; GRB 67: **2.60;** HSF & HWG 65: **3.77** ±0.24 (1-6) in 31; **2.35** ±0.20 (1-6) in 17; **3.02** ±0.15 in 57; **2.9** in 10; RMJ 53: **3.3** ±0.15 in 31; THL 51: **2.82** (1-4) in 11.
Sistrurus catenatus KKA 60: 7; RC 51: 7; HKG 28: 6,

9; HWG & GVO 65: 3, 4, 4, 5, 5, 5, 11; KDK 78: **11.7** in 58; LMK 56: 3, 4, 9, 9; SAM 44: 5; HKR 81: 3, 5, 5, 6, 7, 7, 7, 7, 8, 8, 8, 9; ARR & JQ 47: 9; ECT 41: 11, 11; CAT 55: 9; AHW & AAW 57: 5, 5, 7, 8, 8, 9, 11, 13.

Sistrurus miliarius CCC 60: 32; RRF & JCK 78: 5, 5, 5; JBI 78b: 6, 7, 10; LNK 56: **7.33** (2-18) in 15; 3, 9; 4, 6, 6, 7; WMP & GMW 71: **5.07** (4-7) in 14; MS & RW 59: 5.

Sphenomorphus cherriei HSF 73: **2.24** (1-3) in 29.

Sternotherus minor WAC & KRM 78: **2.4** (1-4) in 107; JBI 78c: **2.43** in 131; DWT 58: **2.7** in 6.

Sternotherus odoratus JWG 70b: 2, 2, 3, 3, 3, 4; JWG 82: **5.6** in 25; JBI 77: **3.21** ±1.34 in 11; IYM & JK 72: **3.0** (2-3) in 13; RJM & KRM 81: **2.8** ±0.19 in 39; **2.6** ±0.15 in 57; DWT 61a: **2.2** (1-4) in 30; **4.6** in 15; RCV, JLB & CJM 82: **3.22** in 58.

Storeria dekayi PA 65: 3, 9, 10, 11, 13, 15, 23, 24; 3, 8, 8, 11; CCC 58: 8, 9, 12; AFC 40: 11; HJC 36: **14.64** ±0.80 (9-20) in 14; JTC 82: 13; RC 51: 9, 10, 12, 15, 23; RFC 49: 11, 15, 16, 17; WED & AS 58: 11; ERF 30: 8; RCF 59: 11, 12, 16; EVG 53: 3; JBI 78b: **9.16** (6-17) in 12; CPK 79a: **14.9** in 30; RHM 45: 4, 8, 16; RHM 75: 31; PWS 61: 5, 6, 12, 17, 23; 8, 24; MS & RW 59: 8, 10, 12; CAT 55: 22; AHW & SCB 15: 12, 17; AHW & AAW 57: **11.8** (3-27) in 28.

Storeria occipitomaculata FNB 37: **7.18** in 77; **7.79** (6-14) in 14; WJB 43: 5, 6, 7, 8, 9, 14, 18; EC 48: 5; RC 51: 3, 15; NSD & IDL 64: **8.25** in 4; RBL & JKJ 48: 3, 11, 13, 13; SAM 44: 6; RDS & GBM 84: **9.0** (2-15) in 31; AHW & AAW 57: 4, 5, 6, 7, 8, 8, 9, 9, 10, 10.

Terrapene carolina HAA 35: **4.2** (2-7) in 60; JKT, RSF & GLP 76: **2.71** in 36.

Thamnophis brachystoma GRP & RCB 70: **7.2** (3-12) in 17.

Thamnophis butleri CCC 52a: 11 in 4; NBF & DWK 83: **11.4** ±0.70 (6-20) in 28; AHW & AAW 57: **8.2** ±1.61 (4-14) in 5.

Thamnophis elegans SJA 81: **10.0** in 68; **8.26** in 56; **13.0** in 15; MME & JH 13: 10; WF 48a: **12.36** in 11; WF 48b: **8.6** (4-14) in 11; FRG 65: 13, 15, 20; WBH 50: **9.7** (9-19) in 28; AGR & HTG 15: 8, 10, 12; AMW 41: 14; AHW & AAW 57:16.

Thamnophis errans RGW 76: 6, 8, 10.

Thamnophis ordinoides WBH 51: **8.8** (3-15) in 44; WF 48b: **6.4** (4-8) in 18; GRS 68: **9.5** (3-20) in 10; JV & JRS 18: 8, 8, 12, 12, 12, 21.

Thamnophis proximus PA 65: 9; GEB 98: 5, 8, 9; CCC 58: 4, 9, 10, 12, 14, 15, 18; DRC 74: 6, 6, 8, 8, 9, 9, 13; JTC 82: 12; RC 65: 8, 9, 10, 10, 13; RFC 49: 11, 12, 13, 15, 17, 24; EVG 53: 9, 12; HKG 28: 6, 8; GEH 42: 12; OPH 92: 9, 12, 20; PWS 61: 11, 12; DWT 57: **13.0** (6-17) in 13; AHW & AAW 57: 6, 12, 17, 27.

Thamnophis radix ESC 45: **13.04** in 33; JTC 82: 20; MME & JH 13: 20; FRG & BPC 59: 17, 21; HKG 28: 13, 27; GEH 42: 19, 21; JBI 75: 13, 21; JCM 44: 13, 17, 18, 25; 37; CHP 44: **14** in 3; PWS 61: **14.6** in 7; RAS & HSF 84: **9.92** in 47.

Thamnophis sauritus JBI 78: 8; RHM 75: 23; SRT 52: 12, 16, 17, 22, 26; OCV 31: 11; AHW & AAW 57: **8.94** ±0.52 (3-20) in 35.

Thamnophis sirtalis AJB 48: 14; FNB & FCB 31: **23.2** in 31; RWB 50: **15.5** in 7; CCC 52: **18.0** in 20; JDC 59: 4, 5, 12, 20, 29; RC 51: 10, 12, 13, 15, 17, 30, 32; 14, 16, 22, 33, 39; RFC 49: 27; NSD & ISL 64: 32; HEE & RMR 51: **25.0** in 14; PTG 77; **16.4** ±1.5 in 14; LHH 70: **18.2** in 42; OPH 91: 35, 39; JBI 78b: 9, 15, 15, 32; EBSL 29 & 30: **25.2** (12-49) in 15; JCL 50: 18; GPM 34: 21; RHM 45: **34.2** (8-48) in 9; GRP & RCB 70: **14.0** (2-17) in 14; AGR 08: 11; NR & BR 60: 10; GRS 68: **11.3** in 7; CAT 55: 36; AHW & AAW 57: **18.6** (7-52) in 43; AHW & SCB 15: 8, 25; MW & JAK 74: 4, 6, 10; WAW & KC 39: 35; DRZ 62: **12.9** in 104; **15.1** in 9.

Trionyx muticus MVP 77: **10.4** ±0.31 (3-26) in 102; **11.6** ±0.76 (3-23) in 22; RGW 62: **18.6** (4-33) in 25; **9.0** (3-25) in 9.

Trionyx spiniferus KMR & GMM 78: **4.8** (9-20) in 5; RCV & JJB 82: **15.28** in 25; RGW 62: **18.95** (9-27) in 21; **9.64** (3-17) in 17.

Tropidoclonion lineatum ERF 30: 2, 7, 8, 9, 11, 12; AHW & AAW 57: 3, 4, 4, 6, 6, 8, 9, 9, 10; JEW 70: 5.

Tropidurus albemarlensis CCC 70: 2, 2, 2, 2, 2; RCS, JML & NWC 67: "usually two . . ."

Tropidurus delanonis DIW 77: **4.36** (3-6) in 36.

Uma notata WWM 65: **2.41** ±0.125 (2-4) in 22; WWM 66a: **2.6** in 90; WWM 66b: **2.19** (1-5) in 90.

Urosaurus graciosus LJV 77: **4.5** (4-5) in 4; **4.7** (4-6) in 6; LJV & RDO 75: **5.3** (3-10) in 23; LJV, RCV & RDO 78: **4.0** ±0.19 (2-8) in 33.

Urosaurus ornatus REB 83: **6.65** in 107; **9.41** in 97; **9.48** in 131; AED 82: **4.7** ±0.1 in 189; **9.0** ±0.2 in 104; **9.0** ±0.2 in 133; **7.1** ±0.3 in 101; CLD 66: 4 (3-5) in 6; FRG 65: 2, 3, 4; LGM 76: **10.5, 7.5;** RFM 77: **5.3** in 262; WSP 73: **4.8** in 24; LJV 77: **6.9** in 10.

Uta stansburiana GB, MC & GLB 83: **3.75** in 194; SRG 77: **3.5** in 162; GAH & FBT 68: **3.25** (1-6) in 521; RAN & LVD 76: **3.33** ±0.08 (2-5) in 87; WSP & ERP 75: **2.85** in 27; **3.41** in 74; **4.39** in 31; **4.82** in 65; **4.21** in 14; **4.00** in 13; **4.00** in 37; **3.78** in 27; **4.48** in 44; **3.31** in 16; DWT 67: **3.91** in 418; **3.22** in 256; RDW 82: **2.5** ±0.38 (2-3) in 8; **3.75** ±0.25 (3-5) in 20; WWT & JMK 72: **3.34** in 12.

Virginia striatula PA 65: 3, 4; CCC 58: 3, 6, 6; DRC & RRF 76: **5.0** (3-9) in 28; EVG 53: 3, 4, 5; JCM 76: 3, 4, 6, 6, 6; MS & RW 59: 2, 5, 6; AHW & AAW 57: 6, 6, 7; 6, 6, 8; RGW 70: 6, 7.

Virginia valeriae PA 65: 2, 2, 7, 8; RSB & TRM 64: **6.8** (5-9) in 9; JEC 58: 4; CSB 03: 5; JTC 82: 6, 7; FG 61: 11, 14; RHM 45: 4, 4, 6, 6, 7, 7, 8; GRP 71: 5, 5, 7, 8; 14; GRP & JTC 71: 4, 4, 6; RMS 51: 6; PWS 61: 5, 5; DJW 63: 4, 5, 6, 9.

Xantusia riversiana RLB, GCG, GAA & YJK 80: **3.25** (3-4) in 4; **4.03** ±0.20 (2-6) in 30; **5.46** ±0.55 in 13.

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